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The genera and subgenera (excluding *Culicoides*) of the Afrotropical Biting Midges (Diptera: Ceratopogonidae)

by

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ABSTRACT

This publication is intended as a guide for the identification of the genera and subgenera of biting and predaceous midges (Diptera: Ceratopogonidae) of the Afrotropical Region. The large and important bloodsucking genus *Culicoides* Latreille is excluded because the Afrotropical species are currently being revised by Rudy Meiswinkel of the Onderstepoort Veterinary Research Laboratory. The taxonomic keys are designed primarily for females, as this is the sex most commonly encountered, and a satisfactory male key has never been devised. Illustrations have been taken from published literature to illustrate key characters. Others have been provided to aid in the recognition of males by genitalia drawings, and when possible, for the immature stages, which are very poorly known except in the genus *Forcipomyia*. A brief diagnosis is presented for the adults and immature stages of each genus (and subgenus) and references are given for available information on biology. Lists are given of included species, or, for the larger genera, of the species described since publication of the Catalogue of Afrotropical Diptera in 1980.

The Afrotropical ceratopogonid fauna comprises a total of 703 species in 50 genera and 19 subgenera. Of these, 15 genera of the tribe Ceratopogonini and one subgenus of *Forcipomyia* Meigen are endemic to the Afrotropical Region. The tribe Ceratopogonini, which has evolved to a remarkable degree in southern Africa, also exhibits strong Gondwanaland relationships, with affinities with the faunas of southern South America and the Australasian Region. Other tribes and subfamilies show a rather generalised pattern of relationships.

CONTENTS

Page

Introduction 28
Taxonomic characters 31
Immature stages 35
Biogeographical considerations 38
Key to genera and subgenera of Afrotropical Ceratopogonidae 40
Synopsis of the Afrotropical Ceratopogonidae 50
  Subfamily Leptoconopinae 50
  Subfamily Forcipomyiinae 55
  Subfamily Dasyheleinae 79
  Subfamily Ceratopogoninae 82
    Tribe Culicoidini 82
    Tribe Ceratopogonini 85
    Tribe Heteromyiini 115
    Tribe Sphaeromiini 119
    Tribe Palpomyiini 132
    Tribe Stenoxenini 137
References 138
Index to genera and subgenera 146

INTRODUCTION

The Ceratopogonidae are widely known as 'biting midges' and include 89 genera and 4,732 species in all regions of the world; 703 species in 50 genera are recorded from the Afrotropical Region. The adults are small flies (length 1–4 mm) that have been little collected and, except for important man-biting species, are very poorly known.

Adult habits are diverse, but the females of most species are adapted to some type of bloodsucking. Those of *Culicoides*, *Leptoconops*, and some *Forcipomyia* (subgenus *Lasiohelea*) species suck vertebrate blood, and are sometimes notorious pests, especially in beach or mountain resort areas. A few are important vectors of disease organisms of man and domestic animals. Some species of *Atrichopogon* and *Forcipomyia* are ectoparasitic on larger insects, whilst those of many genera of Ceratopogoninae are predaceous on other smaller insects. In certain genera such as *Dasyhelea* the adults are exclusively flower-visiting, feeding on nectar, and females of many other ceratopogonids thus supplement their normal blood diet or are non-haematophagous. Because of their flower-feeding habits some small setaceous species of *Forcipomyia* and other genera are important as pollinators of tropical crop plants, including cocoa (Dessart 1961) and *Hevea* rubber.

Because of their small size and flower-visiting habits, many ceratopogonids have been found to be important pollinators of a variety of plants, including several important agricultural crops. Beginning with the pioneer work of Posnette (1950) in Ghana, there followed intensive studies by Dessart (1961 1963) in Zaïre, Kaufmann (1974*a* *b* 1975*a* *b* *c*) in Ghana, and Derron in Saõ Tomé (see Wirth & Derron 1976) on the mechanism and ecology of the pollination of cocoa (*Theobroma cacao* L.) by ceratopogonid midges. In Saõ Tomé the list of ceratopogonid pollinators included 15 species of *Forcipomyia*, four species of *Dasyhelea*, three species each of *Atrichopogon* and *Stilobezzia*, and one species of *Culicoides* (Wirth & Derron 1976). In Ghana Kaufmann (1975*c*) found eight cocoa-pollinating species, of which four were *Forcipomyia*, two *Stilobezzia*, and one each of *Culicoides* and *Atrichopogon*. By far the most important species were the small members of *Forcipomyia* and *Dasyhelea*, with setaceous bodies very efficient in picking up pollen from the stamens and carrying it to the pistils. De Meillon & Wirth (1979*b*) found seven species of *Forcipomyia* and several species of *Atrichopogon* on flowers of avocado (*Persea americana*) in the northern Transvaal.

Blood-sucking ceratopogonids of the genus *Culicoides*, the largest genus in the family, are vectors of various pathogenic organisms in man and other animals, and Kettle (1965), Linley *et al.* (1983), and Linley (1985) have reviewed the available information. Filarial parasites known to be transmitted to man by *Culicoides* include *Mansonella streptocerca* and *M. perstans*, of which *C. austeni* Carter, Ingram & Macfie and *C. grahamii* Austen are proven vectors in tropical Africa, and *M. ozzardi* which is transmitted by *C. furens* (Poey) in the Caribbean area. A series of papers on the relationship between *Culicoides* and the filarial parasites of man in the Cameroun Republic can be found in the Annals of Tropical Medicine and Parasitology for the mid-1950's period (Nicholas 1953 *a b*); Phelps & Mokry (1976) discuss *Culicoides* as filaria vectors in Zimbabwe. Filaria of the genus *Onchocerca* are transmitted to horses and cattle, but the role of *Culicoides* in animal onchocerciasis is still very poorly understood. Arboviruses causing bluetongue of sheep and horsesickness are known to have *Culicoides* vectors in South Africa (du Toit 1944), and midges of this genus are believed to be responsible for the transmission of bluetongue and ephemeral fever of cattle in Kenya (Walker & Boreham 1976) and Nigeria (Herniman *et al* 1983). Several species of *Culicoides* are involved in the transmission of the protozoan blood parasites, *Haemoproteus* and *Leucocytozoon* of birds and *Hepatocystis* of monkeys.

The immature stages occur in varied situations and are poorly known. Some are terrestrial, occurring under bark or on wet or damp wood (*Forcipomyia*), but those of most genera are aquatic, living in mud or sand on the margins of ponds, lakes, or streams, or in tree-holes, water-holding plants, or salt marshes. The early stages of species of *Atrichopogon* and *Dasyhelea* are semi-aquatic, being found on wet alga-covered soil, wood or rocks, and those of some *Culicoides* often occur in wet, decomposing plant material such as banana stalks, rotting fruits, animal droppings, or leaf compost.

Non-taxonomic information on Afrotropical ceratopogonids is sparse and scattered. Mayer (1955) gives some account of their ecology and morphology. An attempt is made here to report what is known about their biology and larval habitats under the respective generic headings.

Earlier taxonomic works on Afrotropical ceratopogonids are much scattered, but special mention should be made of the following, some of which are classic. Carter, Ingram & Macfie (1920 1921*a b*, introductory account, morphology, generic diagnoses, immature stages of West African species); de Meillon (1936 1937 descriptions of many South African species); Clastrier (1958–1984 descriptions and redescriptions of many species, especially from West Africa, Congo, and Seychelles); Cornet (1981 key to genera).

Our key to genera is adapted from the earlier generic keys of Wirth *et al.* (1974 1977) and Wirth & Grogon (1988). There is no comprehensive taxonomic work on the Afrotropical fauna, and a regional monograph for the genus *Culicoides* is especially needed. Useful partial works on *Culicoides*, however, are those of Caeiro (1961) on Angolan species, Khamala & Kettle (1971) on East African species, Glick (1990) on Kenyan species, and revisions of the *similis* Group by Cornet & Chateau (1970), the *milnei* Group by Cornet *et al.* (1974), and 'plain-wing' species by Cornet & Nevill (1980). Colaco (1946) provided a key to the *Culicoides* species of the region, and Fiedler (1951) to those of South Africa, but these works are now largely outdated. Kremer *et al.* (1975) studied some of Goetghebuer's *Culicoides* types. Useful taxonomic works on other Afrotropical genera, or relevant to them, are listed as references under each genus in our present work.

In our discussions of individual genera we may seem to have devoted a disproportionate amount of space to diagnoses and illustrations of the immature stages and to references to biological information. We have intentionally stressed these topics because the biology and immature stages of most Afrotropical species are poorly known and the available accounts are scattered. As the inventory of Afrotropical species progresses towards completion, biological studies will become increasingly important and we hope this synopsis will be useful in promoting biological studies and their application to medicine and agriculture, and preservation of fragile habitats.

To save space and avoid duplication here, in the larger genera, we have referred to the species lists in the 'Catalogue of the Diptera of the Afrotropical Region', (Wirth *et al.* 1980). We have not always repeated these lists in our species inventories, but have only stated the number of species listed in the 'Afrotropical Catalogue' and added lists of 'additions and corrections'.

In the tribe Ceratopogonini our treatment rather closely follows that of the recent publication by Wirth & Grogan (1988), from which many of our illustrations were adapted. We suggest that the serious student of Afrotropical Ceratopogonidae, when using this synopsis, would be greatly aided by the supplementary use of the 'Afrotropical Catalogue' (Wirth *et al.* 1980), the chapter on Ceratopogonidae in the 'Manual of Nearctic Diptera' (Downes & Wirth 1981), and the 'Predaceous Midges of the World' (Wirth & Grogan 1988).

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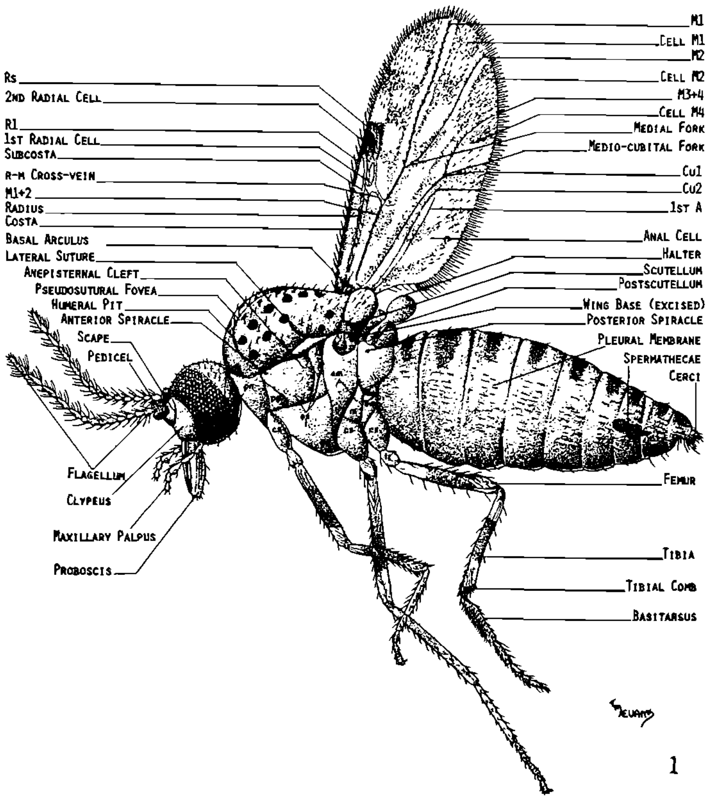
(48), Debenham 1970*b* (322), Downes & Wirth, 1981 (144), Ewen & Saunders 1958 (64–66), Glukhova 1979 (152–154), Goetghebuer & Lenz 1934 (288, 374), Grogan & Wirth 1979 (399–400), Jones 1961 (16–24), Laurence & Mathias 1972 (28, 38–41), Lawson 1951 (10–12), Linley 1970 (17), Macfie 1936 (112), 1939*b* (308, 317–319), de Meillon 1937 (143, 149), 1939*a* (165–166), de Meillon & Downes 1986 (273–274, 279), de Meillon & Hardy 1954 (156–158), de Meillon & Wirth, 1983*b* (289–291), de Meillon & Wirth 1987*a* (170–175, 222–223), Nielsen 1951 (50, 63), Ratanaworabhan 1969 (111, 113, 207–210, 320–321, 323–330, 339–359, 369–373, 375–384, 396–398, 401), Saunders 1956 (70–94, 102–110, 114–115, 127–133), 1964 (116–126), Séguy 1931*a* (359) 1939*b* (391), Thomsen 1937 (164, 385), Williams 1944 (134–142), Wirth 1952*b* (5–9), 1976 (144–151, 155), Wirth & Blanton 1959 (1), Wirth & Grogan 1981 (159, 161–163, 177–179, 199–201, 260–261, 263–265), 1988 (149–163, 180–198, 211–221, 224–254, 271–272, 275–278, 281–287, 302–305), Wirth, Ratanaworabhan & Messersmith 1977 (25).

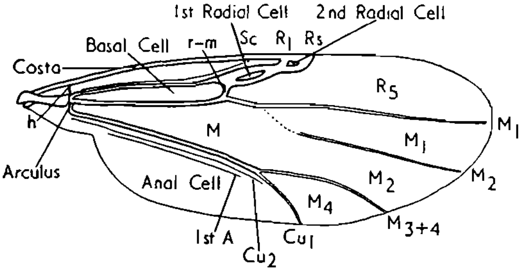
TAXONOMIC CHARACTERS

The Ceratopogonidae are typical members of the dipteran suborder Nematocera and are closely related to the Chironomidae, with which they share many characters. The latter can usually be distinguished from ceratopogonids by the lack of wing vein M2. Good descriptions of the morphological characters of adult ceratopogonids have been published by Carter *et al.* (1920), Edwards (1926), Jobling (1928), Tokunaga (1937*a*), Gad (1951), Wirth (1952*a*), Wirth & Blanton (1959) and Downes & Wirth (1981).

Head: Head (Fig. 3) subspherical to slightly flattened, anterior surface rather flattened and in line with anterior surface of proboscis. Dorsal surface of head consisting of broad posterior occiput and undifferentiated anterior vertex, usually with scattered setae and a row of orbital setae bent over eyes. Eyes bare or with short pubescence between the facets; contiguous above bases of antennae, or more or less separated. Two inconspicuous sensory pits located on frons just above bases of antennae. Frontoclypeus present as a prominent convex sclerite between bases of antennae and proboscis.

Antenna usually 15-segmented, but basal segment or scape reduced to a ring-like segment in head capsule hidden by the enlarged pedicel (in using the keys, the presence of the scape is always implied and included in the count of segments). The 13 divisions of the flagellum are not true morphological segments, but in this paper they are counted as segments in accordance with established custom. First eight segments of ♀ flagellum similar and distinct from the last five, which are usually more elongated. In some genera antennal segments 4–14 are similar. Antennal ratio (AR) is the ratio of the combined lengths of last five segments to the preceding eight. Antennal segments 4–10 of ♀ usually short and typically bearing a basal ring of long verticils (sensilla chaetica) and a subapical pair of hyaline sensilla trichodea; last five usually elongate with basal verticils not so well developed, and usually with scattered short setae and various types of sensilla on distal portion. In some genera segment 3 and/or some of the distal





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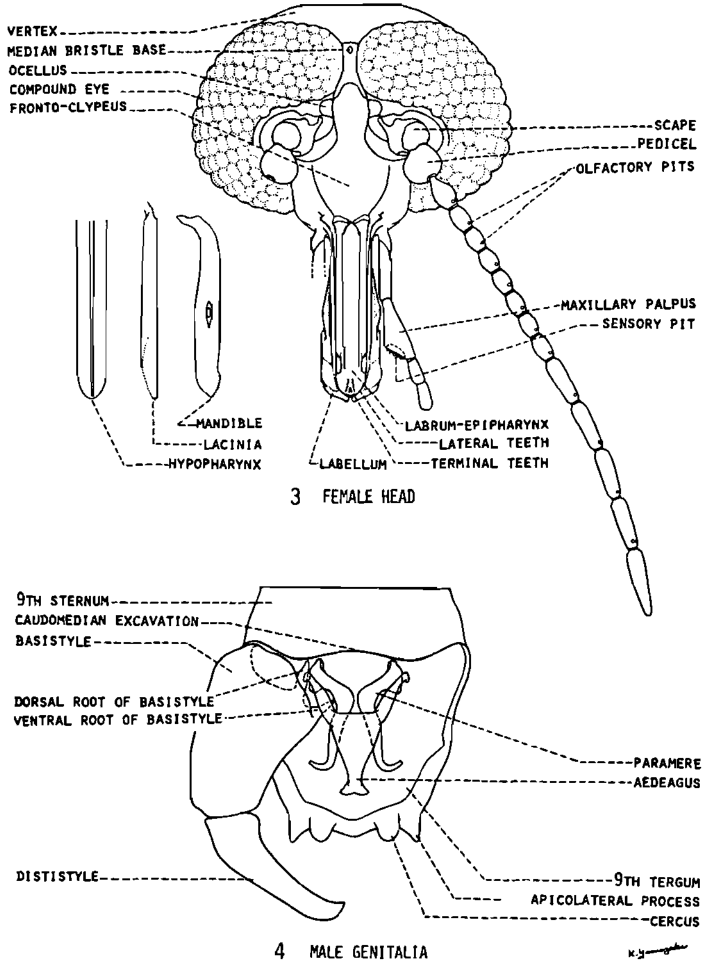
Figs 1–2. *Culicoides* adult morphology: 1, female, lateral view; 2, wing venation.

segments bear one or more sensilla coeloconica ringed by short setulae. The distribution of the sensilla are of great taxonomic usefulness (Wirth & Navai 1978). ♂ antenna more or less plumose, pedicel much larger than in ♀, first nine or ten flagellar segments short and similar, bearing oblique whorls of long verticils, and distal three or four segments much elongated, with short verticils.

Mouthparts (Fig. 3) well developed, stronger in ♀ than in ♂, fitted for piercing and sucking, and forming an elongate proboscis often as long as head. Labium



Figs 3–4. *Culicoides* adult morphology: 3, female head and mouthparts, schematic, parts labelled; 4, male genitalia, schematic, parts labelled.

fleshy with scattered setae, partially enclosing the other six parts, which are slender, distally toothed blades of subequal length. These consist of a strong labrum, a pair of mandibles, a pair of maxillae, and a tubular sclerotised hypopharynx. Maxillary palpi usually 5-segmented in both sexes, setose; third segment usually with median sensory organ and often swollen. A useful character in some genera is the proboscis/head (P/H) ratio, obtained by dividing the distance from the end of the labrum—epipharynx to the tormae, by the distance from the latter to the interocular seta base.

Thorax (Fig. 1): Usually rather broad and convex above, arched anteriorly but not greatly projecting over head, prescutellar area flattened. Pronotum divided into lateral halves by anterior development of mesonotum, partly hidden just below humeri. Mesonotum sometimes bearing small spine or tubercle anteromedially; a pair of small humeral pits often located laterally near anterior margin. Lateral paratergites well-developed in the higher Ceratopogoninae. Scutellum prominent, transverse, usually with bristles; postscutellum arched, bare (except in *Stenoxenus*), with small deep central glandular depression, but without longitudinal division.

Legs: Legs (Fig. 1) usually rather short and stout, with characteristic modifications useful in generic differentiation. One or more pairs of femora may be swollen and bearing prominent ventral spines; tarsomeres may bear spines, or shapes of fourth or fifth tarsomeres may be characteristic; tarsal spine formula as in key and descriptions, expressed as (2–0–2) etc., refers to 2 basal spines, 2 apical, and none in midportion, etc. Presence of long, blunt, black, non-tapering spines or 'batonnets' on ventral side of fifth tarsomeres characteristic of some genera. Shape and development of the claws are extremely important in generic separation, and presence of a well-developed empodium is used to characterise the Forcipomyiinae. The most useful modifications of the fifth tarsomeres and claws unfortunately are found only in the ♀ sex, and thus the ♂ are more difficult to characterise generically without dissecting the genitalia. Hind tarsal ratio (abbreviated TR) is often useful in specific and generic diagnoses, obtained by dividing length of basitarsus by length of second tarsomere.

Wing: Wing (Fig. 2) moderately broad (narrower in ♂) with apex evenly rounded, anal lobe rarely prominent, alula usually without fringe. Wing venation extremely important in generic classification. The Tillyard modification of the Comstock-Needham system of vein designation is followed here (see Fig. 2). The most prominent general features are reduction of the radius to a compact anterior system, fusion of R2 + 3 with R4 + 5 to form radial sector (Rs), termination of R1 and Rs in the costa, and forking of the anterior media and its union to the radius by a crossvein. Costa long or short; one or two anterior radial cells usually present, when present one or the other long or short, reduced; fork of anterior media sessile, petiolate, or interrupted beyond the crossvein. The costal ratio (CR) is obtained by dividing the length of the costa by the wing length, measuring both from the level of the basal arculus of the wing. Posterior veins (M1, M2, M3 + 4, Cu1, Cu2, and 1st A) relatively weak. Development or reduction of the macrotrichia (long setae) or microtrichia (microscopic setae or spicules) and presence of a pattern of pigmented spots or markings are useful. In life, the wings are almost always superimposed and folded flat over the back while the insect is at rest, thus differing in habits from non-biting midges of the family Chironomidae that never superimpose their wings over the back.

Abdomen: ♀ abdomen (Fig. 1) usually short and blunt, somewhat dorsoventrally flattened and terminating in a pair of cerci which are short and rounded, or rarely (in some *Leptoconops*) long and tapered. ♀ genital opening in some genera flanked by modifications of the sterna or an armature of spines or setae. Spermathecae usually strongly sclerotised; their number, size and shape very useful in classification. In the genera of the tribes Palpomyiini and Stenoxenini paired eversible glands open on anterior margins of certain terga; these openings marked internally by tapered sclerotised apodemes ('gland rods') extending anteriorly.

Male Genitalia: ♂ genitalia (Fig. 4) of simple nematocerous type. Rotation of eighth and succeeding segments occurring to greater or lesser degree. Ninth tergum usually an expanded plate, convex externally and hollowed out mesad, and bearing the anus flanked by pair of setose cerci on ventromesal face. Ninth sternum usually much shorter and transverse, with aedeagus projecting caudoventrad from posterior margin. Genital appendages or claspers prominent, forceps-like and 2-segmented; basistyles usually fairly large and simple, bearing a more or less tapered, usually simple, incurved diststyle (except in *Nilobezzia* and *Phaenobezzia*). Aedeagus usually more or less triangular or Y-shaped in ventral view with basal arms articulating with bases of basistyles, flattened and bent in gutter shape in cross-section, convex ventrally and bearing the membranous penis dorsally (internally) with its opening at or near tip of aedeagus. Parameres (claspettes of Snodgrass 1957) typically a pair of submedian processes, often fused, usually symmetrical, articulating with bases of basistyles on dorsal side and projecting distad between aedeagus and ventral face of ninth tergum.

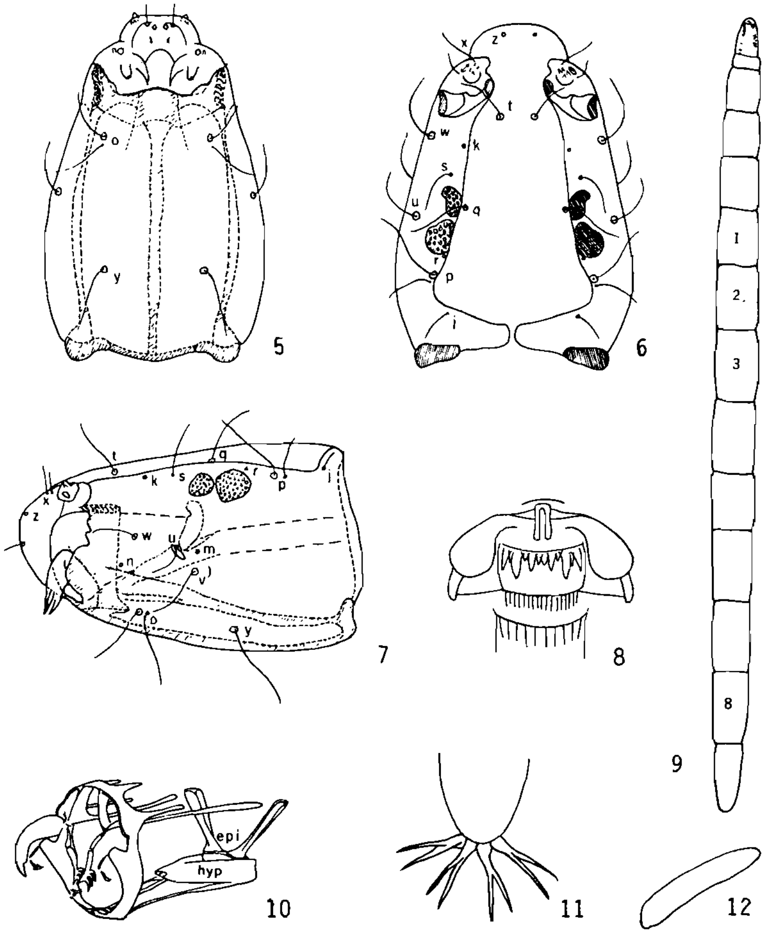
IMMATURE STAGES

Only a few comprehensive studies have been made on the immature stages of Ceratopogonidae. Hennig (1950) reviewed all the published information on immature stages up to that date. Early works that established terminology, especially for the setae and tubercles of the head capsule and body, date from Carter, Ingram & Macfie (1920), Saunders (1924 1925), Tokunaga (1937*a*), Lawson (1951) and Kettle & Lawson (1953). Excellent detailed studies were more recently published by Glukhova (1979) for Ceratopogoninae; Saunders (1956 1959), Nielsen (1951), Ewen & Saunders (1958), and Chan & LeRoux (1965 1970 1971*a*) for Forcipomyiinae; Jamnback (1965) and Nevill (1969) for *Culicoides*; and Clastrier (1972) and Laurence & Mathias (1972) for *Leptoconops*.

Egg: Eggs (Fig. 12) differ markedly among subfamilies; oval to elongate, often black and glossy (Leptoconopinae and Forcipomyiinae), U-shaped and enclosed in a gelatinous cover in Dasyheleinae, and elongate and banana-shaped in Ceratopogoninae, with conspicuous frilled collar on one end in Stenoxenini. They may be deposited on a moist substrate in loose groups (*Forcipomyia*, *Culicoides*, and most other genera), or in strings or masses with gelatinous coating (*Bezzia*, *Mallochohelea*, etc.).

Larva (Figs 5–11): Without functional spiracles. Head sclerotised (except Leptoconopinae), with strong, toothed, non-opposable mandibles; internally with conspicuous pharyngeal apparatus consisting of two strongly diverging arms and a series of combs serving to reduce and sort the food. Three thoracic and nine abdominal segments. Four larval instars. General habitus and structure differ greatly between subfamilies as follows:

Leptoconopinae: Larva (Fig. 38) white or yellow, elongate, smooth. Head prognathous; head capsule (Figs 40, 43–45) not fully sclerotised, with additional internal rod-like structures of uncertain morphology. Thorax and abdomen without conspicuous setae; many segments divided transversely into two subsegments; anal segment with three short lobes.



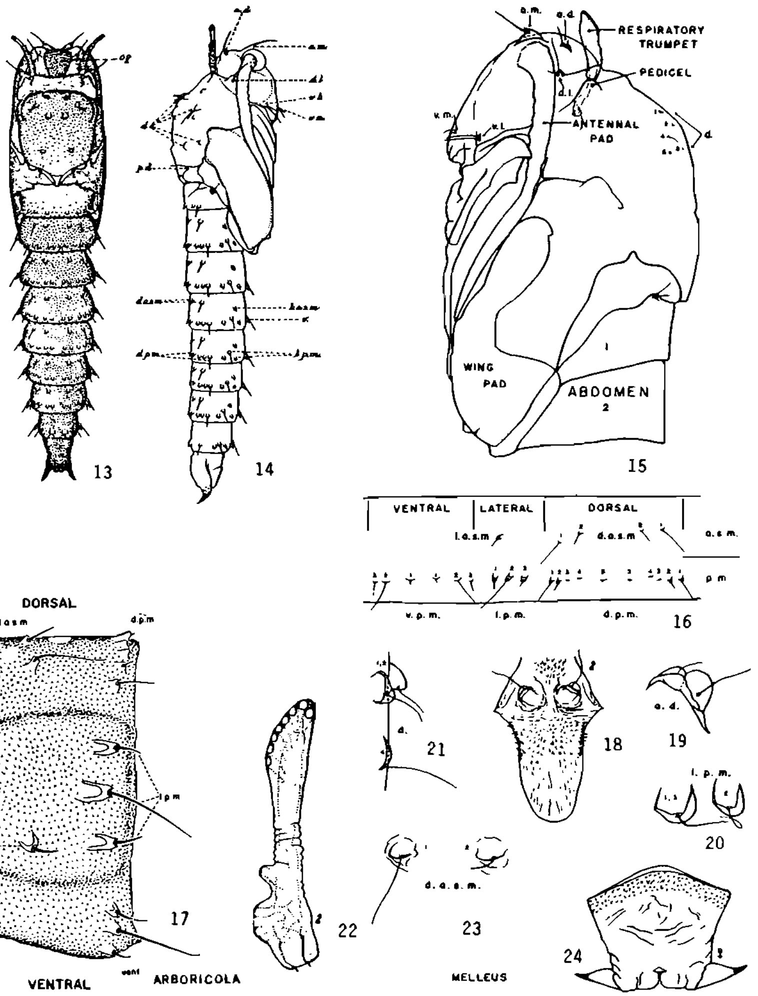
Figs 5–12. *Culicoides* larva and egg: 5–9, *C. melleus* (Coquillett) larva; 5, head, ventral view; 6, head, dorsal view; 7, head, lateral view; 8, hypopharynx, ventral view; 9, larva, lateral view; 10, diagrammatic reconstruction of skeletal structures of *Culicoides* head; 11, lateral view of extruded anal papillae of *C. nubeculosus* (Meigen); 12, *Culicoides* egg (for lettering of setae and for abbreviations see text).

Forcipomyiinae: Larva (Figs 69, 81) reminiscent of *Phlebotomus* (Psychodidae). Head hypognathous. Body segments with conspicuous setae, often complex, set on projecting tubercles; anterior proleg on prothorax simple or bilobed; posterior proleg consisting of a group of hooklets just before anus. On pupation, larval skin usually retained over hind region of abdomen.

Dasyheleinae (Figs 134, 153–154): Head hypognathous or intermediate in position. Body without conspicuous setae or projections; anterior proleg absent; posterior hooklets (Fig. 138) much as those in *Forcipomyia*.

Ceratopogoninae (Figs 5–11): Head prognathous, elongate, and pointed; head capsule well sclerotised. Body setae minute except on last segment; cuticle smooth, whitish or translucent; no prolegs (except for anterior proleg in first instar of some *Culicoides*).

Pupa (Figs 13–24): Appearance relatively uniform, characteristic of the family. Yellowish brown to blackish in colour; usually rather conical in form; body more or less compact, stout anteriorly with pair of prothoracic respiratory horns of diverse structure; last segment usually bearing a pair of pointed terminal processes. Structural details of respiratory horn, operculum (vertex), tubercles bearing spines or setae, and terminal processes of abdomen usually of great diag-



Figs 13–24. Chaetotaxy of *Culicoides* pupae: 13–14, *C. accraensis* Carter, Ingram & Macfie; 15–16, *Culicoides* sp.; 15, cephalothorax, lateral view; 16, diagram of abdominal tubercles; 17, *C. arboricola* Root & Hoffmann, abdominal segment 4; 18–24, *C. melleus* (Coquillett); 18, operculum; 19, 21, thoracic tubercles; 20, 23, abdominal tubercles; 22, respiratory horn; 24, anal segment (for key to abbreviations see text).

nostic value for taxa at all levels. Motion is usually possible by twisting movements of abdomen but not true swimming; air breathing by the anterior horns, aquatic forms hanging at the water surface by non-wettable horns, supported by air bubble beneath wing cases.

BIOGEOGRAPHICAL CONSIDERATIONS

Worldwide, there are 89 genera of Ceratopogonidae, including 4732 valid species. In the Afrotropical Region there are 50 genera with 703 described species. Of these, 11 genera (*Atrichopogon* Kieffer, *Bezzia* Kieffer, *Brachypogon* Kieffer, *Culicoides* Latreille, *Dasyhelea* Kieffer, *Downeshelea* Wirth & Grogan, *Forcipomyia* Meigen, *Leptoconops* Skuse, *Monohelea* Kieffer, *Palpomyia* Meigen, and *Stilobezzia* Kieffer) occur worldwide, with some species in each geographic region. On the other hand, 15 genera are restricted to the Afrotropical Region: *Afrohelea* Wirth, *Ankylohelea* de Meillon & Wirth, *Bothahelea* Grogan & Wirth, *Bothamia* Meiswinkel, *Calcarhelea* Wirth & Grogan, *Capehelea* de Meillon & Wirth, *Ceratohelea* Wirth & Grogan, *Congohelea* Wirth & Grogan, *Fanthamia* de Meillon, *Luciamyia* de Meillon, *Metacanthohelea* Wirth & Grogan, *Neohelea* Clastrier, *Notoceratopogon* de Meillon & Downes, *Paralluaudomyia* Clastrier, and *Stiloculicoides* Wirth & Grogan. One striking fact arises from this list, that all these genera belong to the tribe Ceratopogonini. Worldwide, Wirth & Grogan (1988) list 45 genera in the tribe Ceratopogonini and two have since been described; thus 30% of the genera of this tribe are Afrotropical endemics. There is also an endemic subgenus of *Forcipomyia* in South Africa, but it is the only one from a total of 17 subgenera of *Forcipomyia* occurring in the Afrotropical Region.

An analysis of distribution patterns by subfamily and tribe yields further noteworthy taxonomic and geographic correlations.

Subfamily Austroconopinae. This subfamily, proposed by Borkent *et al.* (1987) for the monobasic genus *Austroconops* Wirth & Lee from West Australia, is an annectant group which may be the sister group of Forcipomyiinae plus Dasyheleinae plus Ceratopogoninae. An alternate hypothesis suggests that *Austroconops* and *Leptoconops* Skuse are sister groups. No Afrotropical species.

Subfamily Leptoconopinae. Represented worldwide by six subgenera and 123 species. Distribution is primarily tropical and subtropical, along seacoasts and in arid regions. The 12 Afrotropical species are fairly evenly distributed in four subgenera, perhaps indicating that their evolution in the Afrotropical fauna occurred in an earlier geological period, with the exception of *Leptoconops spinosifrons* Carter, which may have found its way around the shores of the Indian Ocean and western Pacific at a later date.

Subfamily Forcipomyiinae. Represented by two large worldwide genera that have resisted efforts by taxonomists to break them up into discrete smaller genera. The genus *Forcipomyia* Meigen has been broken up into 25 subgenera with 768 worldwide species; of these 17 subgenera and 134 species occur in the Afrotropical Region. Most of the subgenera of *Forcipomyia* are pantropical or worldwide in distribution; the exception is the endemic Afrotropical subgenus *Rhinohelea* de Meillon & Wirth, containing only two species confined to the southwest Cape Province where their long proboscis is adapted to feeding in the tubular flowers of the *Erica* heath. In *Atrichopogon* Kieffer, with 379 species worldwide, five subgenera have been used by some authors, but the 63 Afrotropical species are not adequately described for subgeneric assignment.

Subfamily Dasyheleinae. One genus, *Dasyhelea* Kieffer, is recognised worldwide, in which some authors recognise four subgenera. These are not well characterised and most of the 440 known species are so poorly described as to render subgeneric assignment impossible. There are 36 Afrotropical species.

Subfamily Ceratopogoninae. The world fauna is arranged in six tribes:

1. Tribe Culicoidini. Two genera in the world fauna. The genus *Paradasyhelea* Macfie with nine described species has a Gondwanaland distribution with one species occurring on the Pacific coast of North America; no Afrotropical species. The large genus *Culicoides* Latreille with 1 153 species worldwide contains 136 Afrotropical species. Species of *Culicoides* occur over all the world with the exception of New Zealand and extreme southern South America.

2. Tribe Ceratopogonini. This tribe, with 50 genera and 854 species worldwide, has 25 Afrotropical genera, and just one-half of all the Afrotropical ceratopogonid genera. The Ceratopogonini enjoys its greatest and most remarkable development in southern Africa, with 15 genera endemic to the region. Moreover, the remaining genera in the tribe are mainly restricted to the southern hemisphere, with 10 endemic to the Neotropical Region, and three genera are endemic to Australia and New Caledonia. Two Gondwanaland genera, *Austrohelea* Wirth & Grogan and *Macrurohelea* Ingram & Macfie, are restricted to Australasia and the temperate Neotropical Region. By contrast, there are only two genera endemic to the Oriental Region, two are Nearctic, and three are Holarctic in distribution.

3. Tribe Heteromyiini. This tribe, with nine genera and 73 species worldwide, is primarily a southern hemisphere group, with 45 species in the Afrotropical, Neotropical, and Australasian Regions. There are four genera in the Afrotropical Region, none endemic, with a total of 14 Afrotropical species. Two genera, *Ceratobezzia* Kieffer and *Physohelea* Grogan & Wirth, are endemic to the Neotropical Region, while the remainder are more widely distributed. Only *Clinohelea* Kieffer occurs worldwide; the Afrotropical Region shares *Neurobezzia* Wirth & Ratanaworabhan with the Nearctic, and *Tetrabezzia* Kieffer with the Oriental Region; *Pellucidomyia* Macfie is pantropical. The occurrence of *Neurobezzia* only in such widely separated localities as California and the Seychelles is anomalous and difficult to explain; perhaps it should be given a closer taxonomic study.

4. Tribe Sphaeromiini. There 21 genera and 321 species worldwide; of these the Afrotropical Region has 12 genera and 73 species. The distribution of the tribe is primarily Old World tropics; there are no endemic Afrotropical genera, but a joint Australasian-Oriental-Afrotropical distribution is shared by three genera (*Homohelea* Kieffer, *Mackerrasomyia* Debenham, and *Neosphaeromias* Das Gupta & Wirth). An Australasian-Afrotropical distribution is shared by one

genus (*Hebetula* Wirth & Debenham), Nearctic-Oriental-Afrotropical by one genus (*Jenkinshelea* Macfie), and Holarctic-Oriental-Afrotropical by one genus (*Macropeza* Meigen). Worldwide genera have the following Afrotropical species: *Mallochohelea* Wirth 12 of 49 species; *Nilobezzia* Kieffer 8 of 64 species; and *Sphaeromias* Curtis 8 of 37 species.

5. Tribe Palpomyiini. There are six genera and 555 species worldwide. In the three large worldwide-spread genera, the Afrotropical Region has 38 species of a total of 262 species in *Bezzia* Kieffer, 27 of 248 in *Palpomyia* Meigen, and 12 of 30 in *Phaenobezzia* Haeselbarth. The three remaining genera of the tribe are exclusively Neotropical: *Amerohelea* Grogan & Wirth with 10 species; *Clastrieromyia* Grogan & Spinelli with four species, and *Pachyhelea* Wirth with one species. The majority of the Palpomyiini species occur in the northern hemisphere, but the Neotropics managed to spin off three small endemic genera.

6. Tribe Stenoxenini. Two highly apotypic genera in this tribe: *Paryphoconus* Enderlein with 38 Neotropical species, and *Stenoxenus* Coquillett with 18 species with pantropical distribution, of which three occur in the Afrotropical Region.

KEY TO THE GENERA AND SUBGENERA OF AFROTROPICAL CERATOPOGONIDAE

(based mainly on females)

1 Wing with crossvein r–m absent (Fig. 25), without macrotrichia; ♀ antenna with 11 or 12 flagellar segments (Fig. 30) (Leptoconopinae, Genus *Leptoconops* Skuse) 2

— Wing with crossvein r–m present, usually with macrotrichia and microtrichia (Fig. 2); ♀ antenna with 13 flagellar segments (Fig. 3)................. 5

2 ♀ abdomen with cerci broader than long (Fig. 31); ♀ antenna with 12 flagellar segments; tarsi (Fig. 34) with strong ventral spines; palpus with definite enclosed sensory pit .... Subgenus **Styloconops** Kieffer

— ♀ abdomen with cerci in form of elongate genital lamellae (Fig. 25); ♀ antenna with 11 or 12 flagellar segments (Fig. 30) tarsi with or without strong ventral spines; palpus with or without definite enclosed sensory pit........ 3

3 ♀ antenna with 11 flagellar segments (Fig. 32); palpus with deep enclosed sensory pit (Fig. 27) .... Subgenus **Holoconops** Kieffer

— ♀ antenna with 12 flagellar segments (Figs 31); palpus with sensory organ superficial (Fig. 26) 4

4 Basitarsi with strong black ventral spines only at apices; ♀ claws each with a prominent basal tooth or seta .... Subgenus **Leptoconops** Skuse

— Basitarsi with black ventral spines 0–0–2 on fore leg, 2–0–2 on midleg, and 0–0–1 on hind leg; ♀ claws each with a long perpendicular seta at base (Fig. 49) .... Subgenus **Proleptoconops** Clastrier

5(1) Empodia well developed, at least in ♀ (Fig. 59); claws strongly curved (Fig. 59); wing usually with numerous macrotrichia (Fig. 70) (Forcipomyiinae) 6

— Empodia small or vestigial (Fig. 172); claws more gently curved (Fig. 185); wing usually with macrotrichia less numerous or absent (Fig. 58) 24

6 Costa reaching well beyond middle of wing, second radial cell usually twice as long as first and with distinct lumen (Fig. 52); microtrichia large and conspicuous, macrotrichia when present scattered, suberect, not scalelike; fringe of posterior border of wing simple, consisting of a single row of alternating longer and shorter setae .... **Atrichopogon** Kieffer

— Costa short or long, second radial cell usually short, but if long is distinctly narrow (Fig. 70); microtrichia minute; macrotrichia moderately abundant, sloping, often scalelike, covering most of wing; fringe complex, not a single row of setae (Genus *Forcipomyia* Meigen) 7

7 Distal six flagellar segments of ♀ antenna elongated (Fig. 111); ♀ empodium large and broad, adapted to clinging to wings of insects (Fig. 112); hind tarsal ratio 3,0 or more .... Subgenus **Pterobosca** Macfie

— Distal four or five flagellar segments of ♀ usually elongated (Fig. 118), rarely all segments short; empodium not greatly enlarged or modified; hind tarsal ratio 0,4–3,2 8

8 Palpus 4-segmented, with only one segment distal to segment bearing the sensory organ (Figs 106, 109) 9

— Palpus 5-segmented (Figs 74, 120) (although segments 4 and 5 incompletely fused in *Euprojoannisia* and some *Caloforcipomyia*) (Fig. 86) 13

9 ♀ with two large functional spermathecae (Fig. 73) 10

— ♀ with one large functional spermatheca (Fig. 119) 12

10 Hind tarsal ratio 0,34–0,40 ...... Subgenus **Pedilohelea** de Meillon & Wirth

— Hind tarsal ratio 1,0–2,0 11

11 Body with deep greenish or bluish subcutaneous pigmentation, especially in abdomen; costal ratio over 0,50; ♂ parameres present ....
Subgenus **Caloforcipomyia** Saunders (part)

— Body without greenish or bluish subcutaneous pigmentation; costal ratio less than 0,50; ♂ parameres absent....... Subgenus **Metaforcipomyia** Saunders

12 ♀ antenna with five distal segments much longer than the short proximal segments; costa long, costal ratio usually about 0,67; hind tarsal ratio 1,30–1,75; ♀ mandibular teeth well developed ....
Subgenus **Warmkea** Saunders

— ♀ antenna with distal segments not much longer than those in proximal series, all segments short ovoid to moderately long tapering; costa variable; hind tarsal ratio variable; ♀ mandibular teeth not developed..............
Subgenus **Saliohelea** Wirth & Ratanaworabhan

13(8) ♀ antennal segments of proximal series compressed, much shorter than distal five, usually transverse (Fig. 111) 14

— ♀ antennal segments of proximal series not much shorter than distal segments and usually not compressed (Fig. 87) 17

14 Costa extending to well beyond middle of wing, second radial cell much longer than first, very narrow (Fig. 116); one subspherical spermatheca present, this without neck (Figs 119); ♀ cibarium armed with denticles; ♀ sucking vertebrate blood .... Subgenus **Lasiohelea** Kieffer

— Costa usually ending at or near middle of wing; second radial cell not unusually long and narrow (Fig. 70); ♀ cibarium unarmed; one or two spermathecae with distinct necks present; not known to suck vertebrate blood . 15

15 Proboscis elongate, from base to clypeus nearly twice as long as height of remainder of head; ♀ with one spermatheca .... Subgenus **Rhinohelea** de Meillon & Wirth

— Proboscis short and stout, less than height of remainder of head; ♀ with two spermathecae 16

16 ♀ suck haemolymph from insects; ♂ empodium present; ♂ parameres U-shaped; larvae breed in moss and wet wood .... Subgenus **Trichohelea** Goetghebuer

- ♀ feeding habits unknown; ♂ empodium usually absent; ♂ parameres H-shaped (Fig. 115); larvae breed in plant leaf axils .... Subgenus **Phytohelea** Remm

17(13) Fourth and fifth palpal segments incompletely fused, immovable (Fig. 86) 18

— Fourth and fifth palpal segments distinctly separated, articulated (Fig. 74) . 19

18 Wing and body with colour pattern and with green or blue subcutaneous pigmentation; antenna unusually elongate and slender .... Subgenus **Caloforcipomyia** Saunders (part)

— Small unmarked grayish species; antenna less elongate .... Subgenus **Euprojoannisia** Brethes

19 Palpus with third segment broadly swollen to past middle, usually nearly to tip, with sensory pit deep, extending nearly to base of segment; slender hyaline peg-like sensory spines present on surface near sensory pore; hind tarsal ratio usually less than 0,5; large species, ♀ suck insect haemolymph .... Subgenus **Microhelea** Kieffer

— Palpus variable, third segment rarely swollen past midlength and not bearing peg-like sensory spines on surface near sensory pore; tarsal ratio usually more than 0,5; size and habits variable 20

20 Small greyish or brownish unmarked species; tarsal ratio usually greater than 2,0; antenna short, proximal segments subspherical, gradually more elongated distally; one spermatheca present 21

— Larger species, often with conspicuous markings on body, legs or wing; hind tarsal ratio usually about 1,0 (0,5–1,5); two well-developed spermathecae present 22

21 ♂ genitalia with club-shaped parameres extending caudad from basistylar apodemes (Fig. 127) .... Subgenus **Synthyridomyia** Saunders

— ♂ genitalia without club-shaped parameres (Fig. 128) .... Subgenus **Thyridomyia** Saunders

22 Body with numerous, conspicuous, flattened scales in addition to normal setae and setae; ♂ genitalia with parameres not joined or fused at bases; dististyle hyaline, elongate, sinuate, parallel-sided or with distinct distal expansion .... Subgenus **Lepidohelea** Kieffer

— Body usually without scales, or if present they are usually not broad; ♂ genitalia with parameres joined or fused at bases, dististyle not expanded distally (Fig. 76) 23

23 ♂ genitalia with aedeagus V-shaped, bearing a pair of small, sharp processes at tip . . . . Subgenus **Schizoforcipomyia** Chan & LeRoux

— ♂ genitalia with aedeagus shield-shaped, with low basal arch (Fig. 76) . . . . . . Subgenus **Forcipomyia** Meigen

24(5) ♂ antennal flagellar segments sculptured (Fig. 150); first radial cell nearly or completely closed, second radial cell usually ending at or before middle of wing, sometimes closed (Figs 148, 149); eyes with short pubescence; ♀ claws small and equal (Dasyheleinae) . . . . **Dasyhelea** Kieffer

— ♂ antennal flagellar segments not sculptured (Fig. 3); either first or second radial cell or both well developed (Fig. 2) (except in some Ceratopogonini); costa ending beyond middle of wing (except in some Ceratopogonini); eyes pubescent or bare; ♀ claws variable (Ceratopogoninae) 25

25 Wing vein M forking beyond r–m crossvein, ie. medial fork petiolate (Fig. 2) (although in *Echinohelea*, with spinose legs, M forks at or near crossvein (Fig. 206); vein M2 sometimes obsolescent basally (Fig. 2) 26

— Wing vein M forking at or before r–m crossvein, ie. medial fork sessile; vein M2 nearly always complete (Fig. 397) 57

26 Claws of both sexes small, equal, and simple (Fig. 1); empodium present but small; proximal tarsomeres with ventral palisade setae (bulbous setae) not aligned in a distinct row; wing with macrotrichia usually abundant (Fig. 1); radial cells both usually well developed, similar in size; prescutal (humeral) pits prominent (Fig. 1) (Culicoidini) . . . . **Culicoides** Latreille

— Claws of ♀ usually larger, equal (Fig. 184) or unequal (Fig. 172); those of ♂ smaller and equal; empodium usually absent; proximal tarsomeres of hind leg at least with one or more distinct rows of palisade setae (Figs 265, 301); first radial cell and more rarely second also, sometimes closed or lost, the second usually much larger than first; prescutal pits small or absent (Ceratopogonini) 27

27 Palpus 4-segmented, only one segment distal to the one bearing the sensory organ (Fig. 284); ♀ costa long, extending nearly to wing tip (Fig. 285); fore and mid coxae of ♂ with dense long spine-like bristles . **Parabezzia** Malloch

— Palpus with five segments, two segments distal to the one bearing the sensory organ (Figs 179, 225); costa variable; ♂ coxae without long spine-like bristles 28

28 Wing with one or both radial cells not formed (Figs 156, 161) 29

— Wing with two radial cells present (Figs 170, 199) 36

29 Wing with both radial cells not formed; claws of fore, mid, and hind legs similar in size; 4th tarsomeres cylindrical; ♂ antenna with segments 4–13 fused . . . . **Brachypogon** subgenus **Brachypogon** Kieffer (part)

— Wing with one radial cell present (Fig. 156); 4th tarsomeres, claws and ♂ antenna variable 30

30 First radial cell present, second not formed (Fig. 211) 31
— Second radial cell present, first not formed (Fig. 159) 32

31 ♀ claws small and equal on fore and mid legs, usually large and unequal on hind leg (Fig. 218); two spermathecae (Fig. 217); ♂ flagellum without plume, distal five segments elongated as in ♀, all segments separate (Fig. 213) ...... **Fanthamia** de Meillon
— ♀ claws of fore, mid and hind legs similar in size; one spermatheca present (rarely two); ♂ antenna with well-developed plume, distal three segments elongated, segments 4–13 usually fused .... **Brachypogon** subgenus **Brachypogon** Kieffer (part)

32 Fore femur with 1–2 short, strong, ventral spines (Fig. 299); fifth tarsomeres with one or two pairs of ventral batonnets (Fig. 301); ♀ claws a single long talon with a slender basal tooth (Fig. 301); ♂ antenna with well-developed plume; pruinose yellowish or brownish species .... **Stilobezzia** subgenus **Eukraiohelea** Ingram & Macfie
— Fore femur unarmed ventrally; fifth tarsomeres without ventral batonnets; ♀ claws equal or unequal; colour and ♂ antenna variable 33

33 Claws on each leg of ♀ unequal, without basal tooth (rarely subequal on fore and midlegs) (Fig. 169); wings with prominent colour pattern or one or more black spots or patches (Fig. 161); ♂ antennal flagellum with normal plume; usually pale yellowish or whitish species with pruinose colour pattern on dorsum of thorax (Fig. 168) and banded legs (Fig. 167) 34
— Claws on at least fore and mid legs of ♀ equal, with or without basal tooth (Fig. 157); wing without prominent colour pattern (rarely a dark area or spot over end of costa); ♂ antennal flagellum with or without plume; usually shiny dark brown species 35

34 Costa short, costal ratio not more than 0,8 (Fig. 161). **Alluaudomyia** Kieffer
— Costa long, extending to wing tip (Fig. 280) ..... **Paralluaudomyia** Clastrier

35 Third antennal segment with sensilla coeloconica (Fig. 178); radial cell short, costal ratio less than 0,65; one spermatheca (rarely two); ♂ flagellum with plume, last three segments elongated, segments 4–13 fused .... **Brachypogon** subgenus **Brachypogon** Kieffer (part)
— Third antennal segment without sensilla coeloconica; radial cell long, costal ratio 0,6–0,8 (Fig. 156); two spermathecae; ♂ flagellum without plume, distal five segments elongated as in ♀, segments 4–13 not fused .... **Afrohelea** Wirth

36(28) Fourth tarsomeres more or less cylindrical (Figs 172, 265) 37
— Fourth tarsomeres cordiform or heart-shaped when viewed ventrally, at least on hind leg (Figs 157, 195) 46

37 Hind femur moderately to greatly swollen, with stout ventral spines in close-set series (Figs 254, 288) 38
— Hind femur sometimes slightly swollen but without stout ventral spines in series (Fig. 246) 39

38 ♀ claws with rounded or straight base, distal portion curved; ♀ hind claws either single and elongate or, if short and equal, lacking inner tooth (Fig. 289); ♂ with more than 0,58 of apex of hind femur bearing strong bristles (Fig. 288) .... **Serromyia** Meigen

— ♀ claws with marked bend at base, distal portion straight; ♀ hind claws short and equal, with well-developed inner tooth (Fig. 253); ♂ with less than 0,43 of apex of hind femur bearing strong bristles (Fig. 254) ....
Metacanthohelea Wirth & Grogan

39 Third antennal segment without sensilla coeloconica or basiconica; wing with or without prominent colour pattern; palpus with small round sensory pit (Fig. 263) 40

— Third antennal segment with sensilla coeloconica or basiconica; wing unmarked, sometimes with inconspicuous infuscation; palpal pit present or absent 43

40 Wing with prominent markings (Fig. 264); ♀ claws equal on fore and mid legs, single on hind leg, with or without basal tooth (Figs 265) 41

— Wing without colour pattern (Fig. 266); ♀ claws similar on all legs, slightly unequal, without basal tooth (Fig. 267) .... **Neohelea** Clastrier (part)

41 Wing usually with four dark areas on anterior margin and with characteristic irregular hieroglyphic markings (Fig. 264); ♀ spermathecae unequal (smaller one usually with long thread-like sclerotisation of duct) (Fig. 259); ♂ aedeagus with sclerotised basal loop joining a pair of strong, sharp-pointed, tapering lateral sclerites (Fig. 260) .... **Monohelea** Kieffer

— Wing with two or three dark areas on anterior margin, continued more or less as bands posteriorly across wing (Figs 160, 199); ♀ spermathecae subequal; ♂ aedeagus without sclerotised basal loop 42

42 ♀ hind claw with basal tooth; hind claw of ♂ a single enlarged talon with basal tooth as in ♀; ♂ aedeagus with distal process borne in a notch in a broad basal sclerite (Fig. 177) .... **Allohelea** Kieffer

— ♀ hind claw without basal tooth; hind claws of ♂ normal, paired, small and equal; ♂ aedeagus a single sclerite not divided into proximal and distal pieces (Fig. 201) .... **Downeshelea** Wirth & Grogan

43(39) Eyes pubescent; antenna short, verticils not prominent (Fig. 178); legs without prominent spines; dark brown species 44

— Eyes bare; antenna elongate with prominent verticils (Figs 209, 210); fore femur with three ventral spines, or legs markedly spiny (Fig. 203); yellowish to reddish brown species 45

44 Second radial cell twice as long as first; costal ratio 0,65; ♂ antenna with segments separate .... **Bothahelea** Grogan & Wirth

— Second radial cell as long as first, costal ratio less than 0,65; ♂ antennal segments 4–13 fused .... **Brachypogon** subgenus **Isohelea** Kieffer (part)

45 Legs with prominent scattered spines (Fig. 203); claws of ♀ equal or unequal, each with basal inner tooth (Figs 204, 205); ♀ sternum 8 expanded into a highly sclerotised genital plate; ♂ antenna with last five segments

elongated as in ♀, without plume (Fig. 209) .... **Echinohelea** Macfie

— Legs without spines except three short, strong, widely spaced, ventral spines on fore femur (Fig. 193); ♀ claws long and equal on fore legs, a single long talon with a slender basal tooth half as long as claw on mid and hind legs (Fig. 194); ♀ sternum 8 not expanded in a highly sclerotised genital plate; ♀ antenna moderately elongate (Fig. 191); ♂ unknown .... **Congohelea** Wirth & Grogan

46(36) Third antennal segment with sensilla coeloconica (Fig. 178); eyes pubescent .... **Brachypogon** subgenus **Isohelea** Kieffer (part)

— Third antennal segment without sensilla coeloconica (Figs 224, 292); eyes usually bare 47

47 Claws of ♀ all equal; fifth tarsomeres unarmed (Figs 184, 247) 48

— Claws of ♀ on at least one pair of legs unequal or reduced to a single long talon with or without basal tooth (Figs 230, 295); fifth tarsomeres often with ventral spines or batonnets (Fig. 295) 50

48 Claws of ♀ without basal inner tooth (Fig. 247); ♀ with costa extending around and behind wing tip, which is bilobed; cell R5 broad distally, vein R4 + 5 joining costa and vein M1 at wing tip (Fig. 240); one spermatheca (Fig. 243); eyes contiguous, bare .... **Luciamyia** de Meillon

— Claws of ♀ with basal inner tooth (Figs 184, 273); costa short, costal ratio 0,45–0,50; venation normal, not as above; two spermathecae; eyes narrowly separated, pubescent 49

49 Costal ratio 0,45-0,50; radial cells small and subequal in length (Fig. 271); spermathecae small and globular with short necks and irregular walls (Fig. 274); ♂ antenna with dense plume, segments 4–12 fused, 13–15 elongated; ♂ ninth tergum about as long as basistyles, with apicolateral processes long, slender, and well separated (Fig. 275); dististyle not abruptly bent at base (Fig. 276) .... **Notoceratopogon** de Meillon & Downes (part)

— Costal ratio 0,62–0,75; second radial cell twice as long as first (Fig. 159); spermathecae oval with smooth walls and long slender necks; ♂ antenna with long sparse verticils not forming a plume, segments 4–12 not fused, 11–14 only slightly elongated, ♂ ninth tergum half as long as basistyle, with apicolateral processes short and close together; dististyle abruptly bent near base, stout and nearly straight distally (Fig. 180) .... **Ankylohelea** de Meillon & Wirth

50(47) ♀ claws equal on fore and mid legs, more or less unequal on hind legs (Fig. 195); eyes setaceous or bare.................................. 51

— ♀ claws usually large and greatly unequal on all legs or a single long talon with a distinct basal tooth (Figs 230, 295); eyes bare 52

51 Hind basitarsus without black spine at base; ♀ hind claws each with basal inner tooth (Fig. 195); eyes of ♂ and ♀ with minute interfacetal setae; antennal segment 14 with sensilla coeloconica; ♂ antenna with dense plume, last three segments elongated, 13th arcuate; necks of spermathecae short and stout.................................. **Ceratohelea** Wirth & Grogan

— Hind basitarsus with black ventral spine at base; ♀ hind claws without basal inner tooth; eyes of ♂ with long interfacetal setae, bare in ♀; antennal segment 14 without sensilla coeloconica; ♂ antenna similar to that of ♀, without plume, last five segments elongated; necks of spermathecae long and slender .... **Calcarhelea** Wirth & Grogan

52(50) First radial cell long and narrow, not rhomboidal; vein M2 interrupted at base (Fig. 226) 53

— First radial cell rhomboidal; vein M2 entire, media with long petiole (Figs 303, 305) 55

53 Hind femur enlarged (Fig. 230); antenna without sensilla coeloconica (Fig. 224); third palpal segment slender with shallow sensory pit (Fig. 225); wing with macrotrichia on distal half, costal ratio 0,60 or more (Fig. 226); ♂ ninth tergum with apicolateral processes greatly enlarged (Fig. 236) ...... **Kolenohelea** de Meillon & Wirth

— Hind femur slender; antenna with sensilla coeloconica on segments 11–14 or 12–14 of ♀; third palpal segment with deep sensory pit; wing and ♂ ninth tergum variable 54

54 Wing with a few macrotrichia on distal half, costal ratio 0,59; eyes closely approximated, bare; ♀ antenna with sensilla coeloconica on segments 12–14; palpus slender, palpal ratio 2,2; spermathecae with irregular surface and a sclerotised collar near neck; ♂ genitalia with prominent apicolateral processes on ninth tergum; aedeagus with one slender distomedian process; parameres separate, distal process straight and slightly enlarged distally with sharp, spurlike, ventromesal projection at tip . **Capehelea** de Meillon & Wirth

— Wing with abundant macrotrichia to base, costal ratio 0,50; eyes separated by width of one facet, pubescent; ♀ antenna with sensilla coeloconica on segments 12–14; palpus short, stubby, palpal ratio 1,2; spermathecae ovoid with smooth surface without collar; ♂ genitalia without apicolateral processes on ninth tergum; aedeagus with two distal processes; parameres joined narrowly in midportion, diverging and blade-like distally...... **Bothamia** Meiswinkel

55(52) Wing with or without ornamentation but not with rounded pale spots on a dark field (Figs 303, 304); palpus slender, third segment elongate (Fig. 293); ♂ antenna with well-developed plume, last three segments elongated; ♂ aedeagus composed of two sclerotised bars in more or less V-shape (Fig. 297); parameres paired, well developed (Fig. 296) spermathecae sclerotised (Fig. 300) (*Stilobezzia* Kieffer, part) 56

— Wing with prominent ornamentation of rounded pale spots on a dark field as in *Culicoides* (Fig. 305); palpus short and stubby, third segment as broad as long (Fig. 305A); ♂ antenna without plume, last five segments elongated as in ♀; ♂ aedeagus a slender rounded arch; parameres reduced to small, paired apodemes; spermathecae unsclerotised .... **Stiloculicoides** Wirth & Grogan

56 Wing with macrotrichia on membrane, at least a few at apex near wing margin (Fig. 304) .... **Stilobezzia**, subgenus **Acanthohelea** Kieffer

— Wing without macrotrichia on membrane (Fig. 303) ....
Stilobezzia subgenus **Stilobezzia** Kieffer

57(25) Tarsomere 5 of ♀ armed ventrally with stout black blunt spines (batonnets) (Figs 321, 343); ♀ abdomen without internal sclerotised gland rods; sternum 8 of ♀ often with pair of setal tufts (Fig. 355) (Sphaeromiini)... 58

— Tarsomere 5 of ♀ unarmed or armed only with slender, sharp-tipped spines (Figs 383, 393, 398); if tarsomere 5 armed, ♀ abdomen with internal sclerotised gland rods (Fig. 401); sternum 8 of ♀ without setal tufts (Fig. 400) 69

58 Tarsal claws unequal, at least on hind leg, or a single long claw with basal tooth (Figs 321, 323, 343).. 59

— Tarsal claws equal on all legs.. 62

59 Tarsal claws unequal on all legs (Fig. 326) 60

— Tarsal claws unequal on four posterior legs, equal on fore leg (Fig. 343) ......
Johannsenomyia Malloch

60 Tarsal claws single with a slender basal tooth (Figs 323); tarsal batonnets variable 61

— Tarsal claws paired, each with blunt external basal tooth (Fig. 321); (three or more pairs of batonnets along length of fifth tarsomere) ... **Dibezzia** Kieffer

61 Mesonotum shining black; fifth tarsomeres with 2–3 pairs of ventral batonnets on basal portion only (Fig. 359); fourth tarsomeres cordiform ....
Hebetula Wirth & Debenham

— Mesonotum densely whitish to greyish pollinose; fifth tarsomere with four or more pairs of ventral batonnets along entire length; fourth tarsomeres cylindrical .... **Xenohelea** Kieffer

62(58) Claws with basal internal and external teeth (Fig. 368); fifth tarsomeres with 12–16 short stout batonnets (Fig. 367); fore femur greatly swollen with 15–20 stout ventral spines (Figs 361) .... **Neosphaeromias** Clastrier

— Claws with basal internal or external teeth, but not both in combination (Figs 373, 379); tarsal batonnets and fore femur variable 63

63 Claws gently curved distally, with slender basal tooth on internal side, if present (Figs 326, 379) 64

— Claws straight or flattened distally (Fig. 343) (gently curved in *M. hansfordi*), with blunt basal external tooth, at least on one pair of legs .66

64 Costa extending to about 0,75 of wing length; fore femur greatly swollen, with numerous short, stout ventral spines (Fig. 351) ....
Mackerrasomyia Debenham

— Costa extending nearly to wing tip (Figs 325, 375); fore femur slender, with or without spines 65

65 Fifth tarsomere basally with 1–2 pairs of batonnets (Fig. 326) ....
Homohelea Kieffer

— Fifth tarsomere with three or more pairs of batonnets along entire length of segment (Fig. 379)............................... **Sphaeromias** Curtis

66(63) Costa short, extending to 0,75–0,87 of wing length (Fig. 354) 67

— Costa long, extending nearly to wing tip; costal ratio over 0,9 (Fig. 347) . 68

67 Two radial cells; wing grayish hyaline, veins usually infuscated, anterior veins prominent (Fig. 354); mesonotum usually shining yellow to black with little or no pollen; palpus usually with fifth segment as stout as fourth; ♂ genitalia with well-developed basistyle and articulated dististyle; ♀ ninth sternum not forming two sclerotised bars .... **Mallochohelea** Wirth

— One (rarely two) radial cell(s), wing usually whitish, anterior veins usually pale and not prominent, wing usually whitish; mesonotum dull, usually with dense whitish to greyish pollen; palpus tapering distally, fifth segment more slender than fourth; ♂ genitalia with short, stout basistyle and immovable, bud-like dististyle; ♀ ninth sternum forming two sclerotised bars .... **Nilobezzia** Kieffer

68(66) Wing with large angular anal lobe (Fig. 331) .... **Jenkinshelea** Macfie

— Wing with small anal lobe (Fig. 347) .... **Macropeza** Meigen

69(57) Fore fifth tarsomere usually inflated (Fig. 312); claws of ♀ usually unequal, at least on hind leg, or only a single claw present with or without basal tooth (Figs 313, 317); ♀ abdomen without internal sclerotised gland rods (Heteromyiini) 70

— Fore fifth tarsomere slender; claws of ♀ equal on all legs (Figs 393, 398); ♀ abdomen with internal sclerotised gland rods dorsally (Fig. 401)...... 73

70 Costa prolonged beyond tip of vein R4+5; media barely sessile (Fig. 315); fifth tarsomere of fore leg not inflated (Fig. 307); one radial cell present; claws equal on fore and mid legs, unequal on hind leg .... **Neurobezzia** Wirth & Ratanaworabhan

— Costa not prolonged beyond tip of vein R4+5, media broadly sessile (Figs 314, 320); fifth tarsomere of fore leg inflated; radial cells and tarsal claws variable 71

71 Fourth tarsomere cylindrical, not divided into spinose bifid lobes (Figs 317–319); (fifth tarsomere of fore legs inflated, fusiform; claws equal on fore and mid legs, hind leg with one long talon and a much weaker second talon (Fig. 317); wing milky; body densely pollinose).. **Pellucidomyia** Macfie

— Fourth tarsomere ending in two bifid lobes armed with spines, at least on one pair of legs (Fig. 311); fifth tarsomeres, claws and wing variable) 72

72 Claws equal on fore leg (Fig. 312), unequal on mid and hind legs (Fig. 313); fifth tarsomere of fore leg greatly swollen (Fig. 312); fourth tarsomere with bifid spinose lobes on mid and hind legs (Figs 311, 313), cordiform on fore leg (Fig. 312); one or two radial cells................... **Clinohelea** Kieffer

— Claws unequal on all legs (Fig. 324); fifth tarsomere of fore leg not greatly swollen; fourth tarsomere with bifid spinose lobes on all legs (Fig. 324); one radial cell (Fig. 320) .... **Tetrabezzia** Kieffer

73(69) Body unusually slender and dorsoventrally flattened; wing (Fig. 390) with one very narrow radial cell; costa extending nearly to wing tip and vein M2 strikingly elbowed at base in ♀, normal in ♂; palpus 4-segmented (Fig. 392);

eyes broadly separated (Fig. 396); legs long and slender, with fine setae; femora unarmed; claws very short (Fig. 393) (Stenoxenini) .... **Stenoxenus** Coquillett

— Body not unusually slender or dorsoventrally flattened; wing with one or two radial cells, if these are narrow, costa not extending nearly to wing tip (Figs 382, 397); crossvein r–m longer; vein M2 normal; palpus 5-segmented (Fig. 381); eyes narrowly to moderately separated; legs not unusually long; femora often armed; claws of ♀ usually moderately long (Figs 383, 398) (Palpomyiini) 74

74 Two radial cells present (Fig. 397); fore femur with strong ventral spines and usually more or less swollen .... **Palpomyia** Meigen

— One radial cell present (Fig. 382); fore femur variable 75

75 Femora unarmed; costa longer, costal ratio 0,82–0,87; ♀ fifth tarsomeres with stout ventral setae with sharp, bent tips (Fig. 383); ♂ dististyle short and not articulated, or absent (Fig. 384) .... **Phaenobezzia** Haeselbarth

— Femora usually armed, at least on fore leg; costa short, costal ratio 0,67–0,75; fifth tarsomeres of ♀ usually without ventral setae (Fig. 398); ♂ dististyle well developed, articulated (Fig. 388) .... **Bezzia** Kieffer

SYNOPSIS OF THE AFROTROPICAL CERATOPOGONIDAE

SUBFAMILY LEPTOCONOPINAE

Note: Only one genus, *Leptoconops* Skuse, in the subfamily. Opinions differ on the status of Leptoconopinae as a subfamily of Ceratopogonidae or its recognition as a separate family of Diptera. Recently Borkent *et al.* (1987) made a cladistic study of *Leptoconops* and *Austroconops* Wirth & Lee, resulting in the placement of the Leptoconopinae as the earliest lineage of Ceratopogonidae, followed next in order of phylogenetic sequence by Austroconopinae, Forcipomyiinae, Dasyheleinae, and Ceratopogoninae.

Genus *Leptoconops* Skuse

Synonymy under subgeneric headings.

References: Carter, 1921: 1 (revision); Clastrier, 1972: 309 (immature stages of *L. kerteszi*); Wirth & Atchley, 1973: 1 (subgenera: revision North American species); Clastrier & Wirth, 1978: 1 (general taxonomy; revision of North American species of *kerteszi* Group); de Meillon & Wirth, 1983*a*: 348 (key to Afrotropical species).

Diagnosis: Small, dark-coloured midges with pale wings (Fig. 25). Differ from other ceratopogonids as follows: Eyes widely separated in both sexes; frons well developed (Figs 31–32). Only the apical flagellar segment of antenna elongated and sharply differentiated (Fig. 29); 13 flagellar segments in ♂, 11 or 12 in ♀. Palpus with characteristic fusion of segments 4 and 5, appearing 4-segmented (Figs 26–27). Wing (Fig. 25) lacking macrotrichia on membrane and veins; radial system short, well pigmented, but not developed as normal rib-like sclerotised veins; a long intercalary vein of uncertain origin present; crossvein r–m absent; posterior veins typical but faint. In ♀ cerci large, usually elongate and triangular (Fig. 25). In ♂ basistyles approximated at bases; dististyle ending in a small articulated denticle, unique in Ceratopogonidae (Figs 36–37, 47–48).

Immature stages: Larva (Fig. 38) whitish, yellowish, to bright orange; elongate, smooth. Head (Fig. 40) prognathous; head capsule (Figs 43–45) not fully sclerotised, setae and sensilla poorly developed; mandible well sclerotised, with three teeth; internally with rod-like structures of uncertain morphology. Thorax and abdomen with greatly reduced setae; many segments divided transversely into two subsegments (Fig. 38); anal segment with three short lobes. Pupa (Fig. 41) short and stout compared to other ceratopogonids; respiratory horn (Fig. 41) short and broadly rounded, at most 1,5 times as long as broad, with row of 4–20 spiracular openings around apex; thoracic setae inconspicuous; abdomen with short stout setae arising from strong tubercles; last abdominal segment with a pair of blunt, poorly sclerotised lobes, sometimes bent distolaterally.

Biology: Females usually suck vertebrate blood; typically diurnal biters. Larval habitats typically are sandy margins of coastal lagoons sheltered from wave action, seepage areas in desert oases, wetter portions of salt flats, or margins of vernal ponds in arid regions.

Subgenus *Holoconops* Kieffer

(Figs 25, 27, 29–30, 32–33, 35, 37, 43–45, 49)

Holoconops Kieffer, 1918: 135. Type species, *Leptoconops kerteszi* Kieffer, by original designation. Reference: Clastrier, 1981*a*: 87 (Afrotropical species).

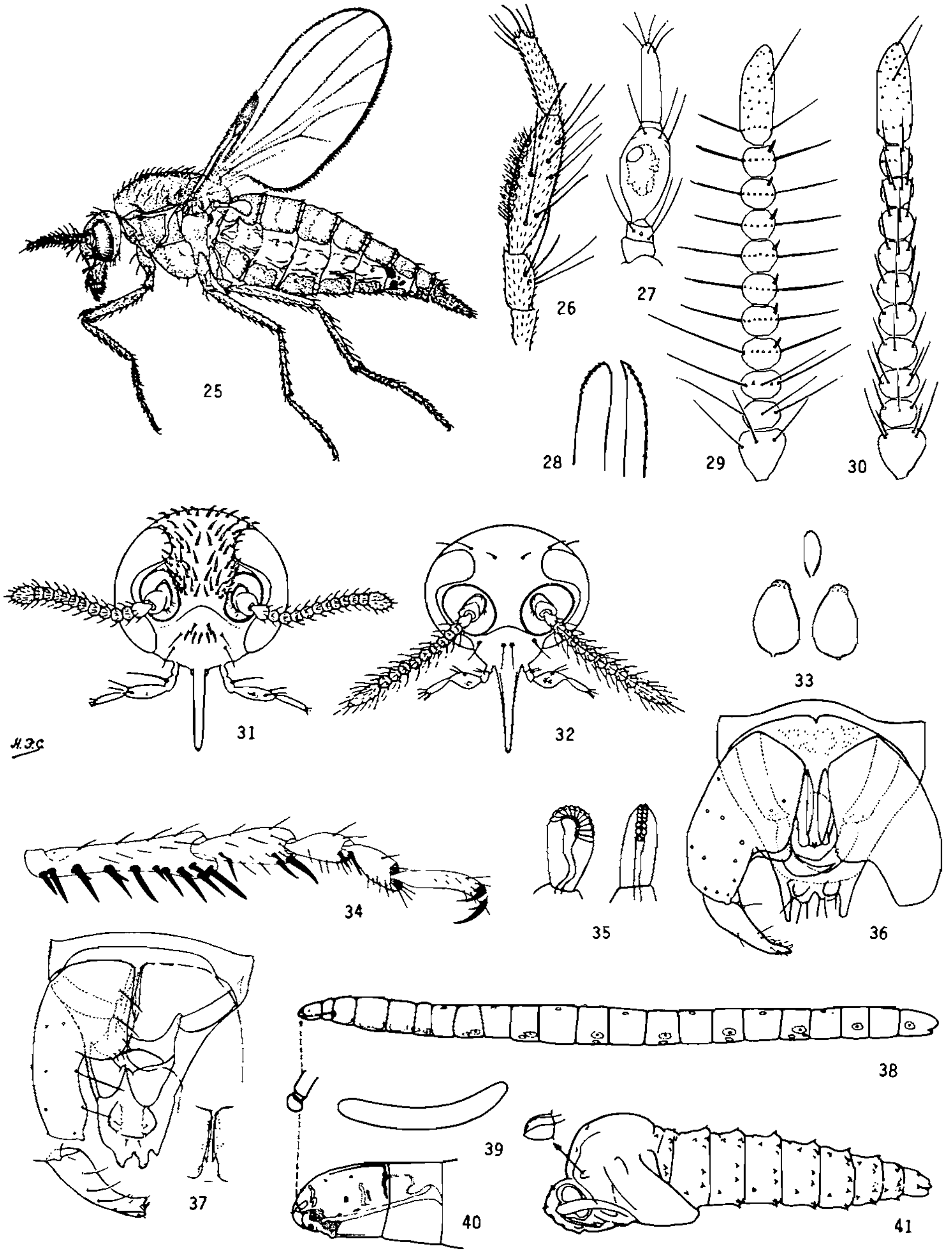
Diagnosis: ♀ antenna (Figs 29–30, 32) with 11 flagellar segments. Frons and vertex without scattered spines or setae, but with a row of setae (Fig. 32). Palpus with sensory area confined in a pit with small pore (Fig. 27). ♀ tarsal claws without basal tooth (Fig. 49). Tarsi with a few moderately strong ventral spines on basitarsi and at apices of distal tarsomeres. ♀ genitalia with long tapering cerci (Fig. 25). ♂ ninth tergum narrowed distally with a closely approximated pair of submedian processes (Fig. 37).

Biology: Clastrier (1981*a*) stated that adults of *L. nevilli* were collected in emergence traps along brackish streams at Northeast Cape. *Leptoconops umbellifer* was taken in a handnet while swarming over sedges on the edge of a salt lake at Zoutpan near Pretoria, Transvaal. According to Nevill (1975) *L. nevilli* breeds in sand in river beds where the moisture content varies between 10 % and 13 % with a pH of 8,6 and a high salt content.

Distribution: Worldwide except Australasian Region; 51 species.

Afrotropical species:
auster Clastrier, 1981*a*: 91. South Africa.
interruptus Enderlein, 1908: 460 (*Mycterotypus*). Namibia.
nevilli Clastrier, 1981*a*: 88. South Africa.
umbellifer Clastrier, 1981*a*: 93. South Africa.

Remarks: *Leptoconops kerteszi* Kieffer (1908: 576) was described from Egypt and later was reported by various authors from southern Europe, Africa, and western North America. Clastrier (1973*a* 1973*b* 1981*b*) and Clastrier and Wirth (1978) revised the '*kerteszi* Group', recognizing numerous distinct species in each geographic region. The species *L. kerteszi* remains an enigma as no type material exists and the brief original description indicates that it may be a valid species



Figs 25–41. *Leptoconops* spp.: 25, 32, *L. (Holoconops) americanus* Carter; 26, *L. (L.) stygius* Skuse; 27, 29–30, 33, 37, *L. (H.) nevilli* Clastrier; 28, 31, 38–41, *L. (Styloconops) spinosifrons* (Carter); 34, *L. (S.) albiventris* (de Meijere); 35, *L. (H.) kerteszi* Kieffer; 36, *L. (Proleptoconops) dixi* de Meillon; 25, female habitus; 26, 27, female palpus; 28, female mandible and maxilla; 29, female antenna, internal view; 30, same, external view; 31–32, female head, anterior view; 33, spermathecae; 34, female fore tarsus; 35, pupal respiratory horn, two views; 36, 37, male genitalia; 38, larva; 39, egg; 40, larval head and prothorax; 41, pupa.

very near *L. peneti* Langeron, known only from its type locality. Previous South African records of *L. kerteszi* probably refer to *L. nevilli* Clastrier.

Subgenus *Leptoconops* Skuse

(Figs 26, 48)

Leptoconops Skuse, 1889: 288. Type species, *Leptoconops stygius* Skuse, by monotypy.

Reference: Clastrier, 1983*d*: 297 (revision Afrotropical species).

Diagnosis: Antenna of ♀ with 12 flagellar segments. Frons bare, rarely with 1–2 setae; vertex with row of setae. Palpus with sensilla scattered over mesal surface or confined to a large open depression on third segment (Fig. 26). Tarsi with strong ventral spines only at apices of basitarsi. ♀ claws simple or dentate. ♀ genitalia with long tapering cerci. ♂ ninth tergum with a pair of slender, digitiform apicolateral processes (Fig. 48).

Biology: Clastrier (1983*d*) reported biting habits of *L. capensis* near Pretoria, Transvaal: Collected by Nevill at face of man on cattle ranch, and collected by handnet around heads of man and cattle and inside of ears; and near Windhoek, Namibia, on cattle, around ears.

Distribution: Worldwide; 55 species.

Afrotropical species:
capensis de Meillon & Hardy, 1953: 24. South Africa.
demeilloni Clastrier & Nevill, 1984: 245. South Africa.
harrisoni de Meillon & Hardy, 1953: 22. South Africa.
nicolayi de Meillon, 1937. 330. Zaïre.
rhodesiensis Carter, 1921: 14. Zambia.

Genus *Proleptoconops* Clastrier

(Fig. 36)

Leptoconops, subgenus *Proleptoconops* Clastrier, 1974: 231. Type species, *Leptoconops hutsoni* Clastrier, by original designation.

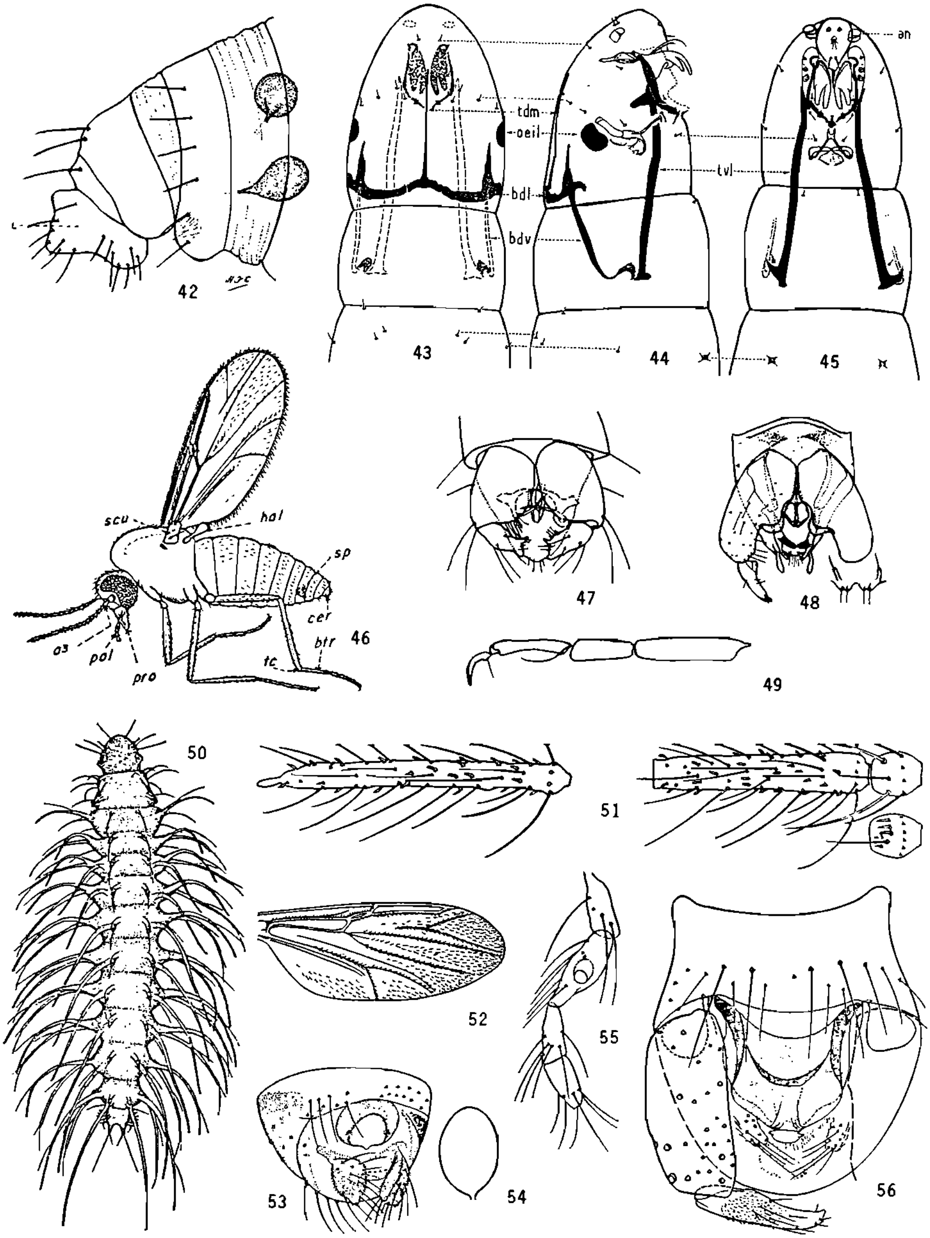
Reference: Clastrier & Boorman, 1987: 293 (taxonomic notes on 6 species).

Diagnosis: ♀ antenna with 12 flagellar segments. Frons and vertex without strong spines. Palpus with sensory organ superficial. ♀ claws each with a long perpendicular seta at base. Basitarsi with black ventral spines 0–0–2 on fore leg, 2–0–2 on midleg, and 0–0–1 on hind leg. ♀ abdomen with elongate lamellae. ♂ genitalia (Fig. 36) broader than long; ninth tergum with well-developed apicolateral processes. Immature stages unknown.

Biology: *Leptoconops dixi* females were taken biting man at Rooibank, an isolated water hole in the desert east of Walvis Bay, Namibia. Clastrier (1983*d*) reported that this species was collected by handnet off horses near Prieska, Northwest Cape.

Distribution: Africa, Eurasia, North America; 7 species.

Afrotropical species:
dixi de Meillon, 1936: 141. Namibia, South Africa.
fuscipennis Clastrier, Rioux & Descous, 1961: 93. Chad.



Figs 42–56. *Leptoconops* and *Atrichopogon* spp.: 42, 47, *Leptoconops spinosifrons*; 43–45, *L. kerteszi* Kieffer; 46, *Atrichopogon* sp.; 48, *L. (L.) demeilloni* Clastrier; 49, *L. nevilli*; 50, *Atrichopogon hexastichus* Nielsen; 51–56, *A. lampronotus* (Kieffer); 42, female abdomen, posterior segments; 43, dorsal, 44, lateral, and 45, ventral view of larval head and prothorax; 46, female habitus; 47–48, 56, male genitalia; 49, male fore tarsomeres 3–5; 50, larva; 51, female antennal segments 10–11, 15; 52, female wing; 53, female genitalia; 54, female spermatheca; 55, female palpal segments 2–5.

Subgenus *Styloconops* Kieffer

(Figs 28, 31, 38–42, 47)

Styloconops Kieffer, 1921*a*: 107. Type species, *Leptoconops albiventris* de Meijere, by original designation.

Acanthoconops Carter, 1921: 24. Type species, *Acanthoconops spinosifrons* Carter, by original designation.

References: Duval 1971: 203 (biology, control); Laurence & Mathias 1972: 51 (biology, immature stages, figs.; Seychelles).

Diagnosis: Antenna of ♀ with 12 flagellar segments (Fig. 31). Frons and vertex with numerous spines or short setae (Fig. 31). Palpus with sensory area confined in a pit with small pore. Tarsal claws with small basal tooth (Fig. 34). Basitarsus and sometimes second tarsomere armed ventrally with prominent spines (Fig. 34). ♀ genitalia with short lamellae (Fig. 42). ♂ genitalia short and broad; ninth tergum simple distally, without apicolateral processes (Fig. 47).

Immature stages: (Figs 38–41, after Laurence & Mathias 1972: 51). Larva of *L. spinosifrons* with mandibular teeth short; no pigmentation or setation visible on thorax or abdomen. Pupa transparent yellowish brown; respiratory horn short, as broad as long, with 4–5 spiracular openings.

Biology: *L. spinosifrons* is a widespread bloodsucking pest around the seashores of the Indian Ocean and southwestern Pacific. It breeds in wet sand in the flat or backward sloping beach between high tide mark and the vegetation fringing the back of the beach.

Distribution: Shores of Old World tropics; 8 species.

Afrotropical species:

spinosifrons Carter, 1921: 24 (*Acanthoconops*). Tanzania (Zanzibar); Madagascar, Seychelles, Oriental Region.

SUBFAMILY FORCIPOMYIINAE

References: Chan & LeRoux, 1971*b*: 1323 (phylogenetic relationships); Debenham, 1987*d*: 631 (taxonomic discussion, phylogenetic diagram).

Diagnosis: Wing (Fig. 70) with numerous macrotrichia, costa short to moderately long. Empodium well developed, at least in ♀; claws strongly curved (Fig. 59). Larva (Figs 69, 81) with anterior and posterior prolegs; body usually with well-developed spines and/or setigerous processes; head more or less hypognathous with well-developed antenna and mouthparts; pharyngeal skeleton with about six combs. Pupa (Figs 68, 77) usually with larval exuviae attached to last three segments.

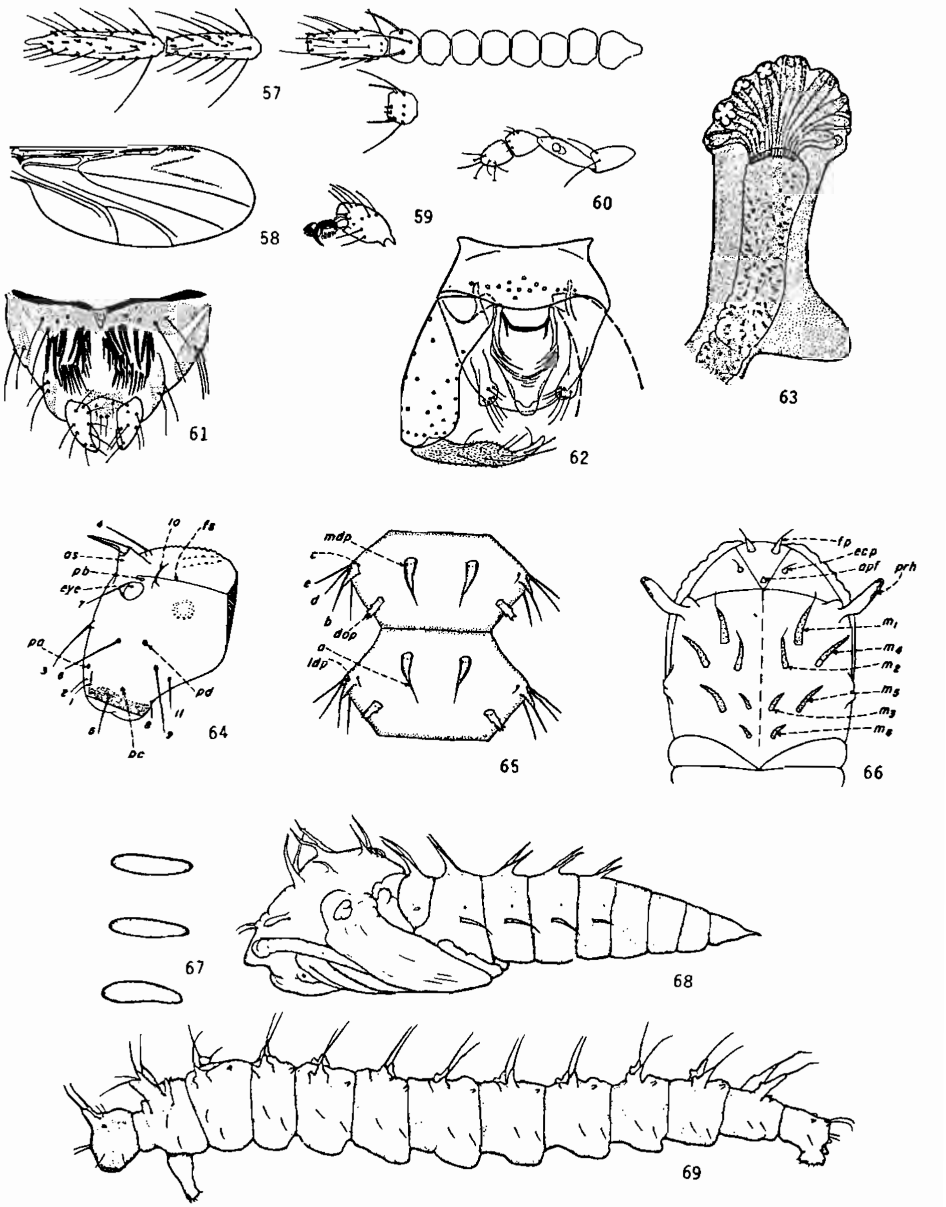
Genus *Atrichopogon* Kieffer

(Figs 46, 50–69)

Atrichopogon Kieffer, 1906: 53. Type species, *Ceratopogon exilis* Coquillett, [= *Atrichopogon levis* (Coquillett)], by designation of Coquillett, 1910: 512.

Note: Several subgenera have been proposed and used for the Nearctic and Palaearctic *Atrichopogon*, but their use has been limited because of the difficult taxonomy and inadequately described older species; subgenera are not recognised here for the Afrotropical species.

References: Nielsen, 1951: 1 (morphology; taxonomy; immature stages; Denmark); Ewen & Saunders, 1958: 671 (revision based on all stages).



Figs 57–69. *Atrichopogon* spp.: 57–62, *A. trichotomma* (Kieffer); 63, *A. alveolatus* Nielsen; 64–66, *Atrichopogon* sp.; 67–69, *A. geminus* Boesel; 57, female antennal segments 3–11, 14–15; 58, female wing; 59, female mid leg tarsomere 5; 60, female palpal segments 2–5; 61, female genital armature; 62, male genitalia; 63, pupal respiratory horn; 64, larval head; 65, abdominal segments 1 and 2 of larva; 66, pupal cephalothorax; 67, eggs; 68, pupa; 69, larva.

Diagnosis: Small to large midges (Fig. 46); body short and stout, slightly setaceous. Eyes pubescent or bare. ♀ antenna with last five segments cylindrical, segments 4–10 globular or transverse, last segment with terminal style or nipple (Figs 51, 57). Palpus (Figs 55, 60) usually rather stout, 5-segmented; third segment usually with deep sensory pit opening by smaller pore. ♀ mandible with numerous teeth. Mesonotum bare or with only short setae. Legs slender with few or no long setae, femora rarely armed ventrally; end of fore femur with setose anterior lobe; hind basitarsus at least twice as long as second tarsomere. Claws (Fig. 59) stouter than in *Forcipomyia*, those of ♀ often cleft or tripartite apically. Wing (Fig. 52) broad, anal angle more rounded than in *Forcipomyia*. Microtrichia large, macrotrichia less dense and more erect than in *Forcipomyia*, usually setiform, often confined to wing tip or absent, usually much reduced in ♂. Costa usually reaching to two-thirds wing length; second radial cell long, usually well formed, a conspicuous intercalary fork or forked fold in cell R5. ♀ abdomen often with median appendage or cluster of spines on sternum 7 and/or 8 (Fig. 61); one or two spermathecae (Fig. 54). ♂ genitalia (Figs 56, 62) with short ninth sternum; tergum usually rounded, without processes; aedeagus usually simple, usually trilobed; parameres absent, basistylar apodemes hook-shaped.

Immature stages: Larva (Figs 50, 69) small (1–4 mm long); similar to that of *Forcipomyia*. Head capsule (Fig. 64) strongly sclerotised, often with sculpture of strong tubercles or spinules; antenna spurlike, borne on large conical protuberance; mouthparts well developed, pharyngeal skeleton with about six combs, pharyngeal angulus with bristles; 11 pairs of setae on head capsule usually well developed (letter designations (Fig. 64) after Ewen & Saunders (1958) corresponding to Saunders (1924) for *Forcipomyia*). Body segments (Fig. 65) usually appear flattened due to extension of the sides into lateral processes of variable extent and shapes; setose dorsal processes may also be developed. Anterior and posterior prolegs well developed. In some species each body segment also with various elliptical membranous respiratory areas; integument of body variably micro-spinose or sculptured, and in life the larva usually bears a coating of debris collected between the processes. Pupa (Fig. 68) small, up to 4 mm long, stout anteriorly, tapering caudad to a pair of conical to slender caudal processes; larval exuviae retained on abdomen of pupa. Sides and dorsum of pupa (Fig. 66) with variety of short to long tubercles or processes characteristic of each species. Respiratory horn (Fig. 63) more or less flattened, narrowed at base, moderately stout but with swelling on dorsal side near base; spiracular openings arranged variably, sometimes complex.

Biology: Adult habits vary. Females of subgenus *Meloehelea* suck haemolymph from beetles, usually of families Meloidae or Cantharidae; those of other groups often attracted to cantharidin. Some species (especially of subgenus *Psilokempia*) are attracted to flowers in large numbers, and females of a few species pierce pollen grains and suck the pollen sap. Females of *A. nilssoni* were observed feeding on pollen of male flowers of an aroid plant in Madagascar. Larvae are aquatic or semi-aquatic, found on the surface of mud, wet wood, or stones, feeding on micro-organisms such as diatoms and other algae. Mayer (1955) described the immature stages of *A. victoriae* de Meillon which were collected in the Berg River, Cape Province, on stones at the margin of shallow water. *Atrichopogon homoius* Ingram & Macfie was reared from material taken from a canoe, and *A. ochrosoma* (Ingram & Macfie) was reared from plants of the water lettuce, *Pistia stratiotes* L.

Distribution: Worldwide; 345 species.

Afrotropical species: The Afrotropical Catalogue (Wirth *et al.* 1980) lists 55 species; additions and corrections:

distictus Kieffer, 1918: 43 (South Africa; Zimbabwe, Zaïre (not *distinctus*).
falcis de Meillon & Wirth, 1981*c*: 571. South Africa.
helles de Meillon & Wirth, 1983*a*: 350. South Africa.
luteicollis Becker, 1903: 74 (*Ceratopogon*). Egypt; Sudan, South Africa (synonyms: *aegyptius* Kieffer, 1925*b*: 250 (Egypt); *phrixius* de Meillon, 1943: 105 (South Africa).
nilssoni de Meillon & Wirth, 1989*a*: 88. Madagascar.
quadrisetosus Goetghebuer, 1933: 141 (*Stilobezzia*). Zaïre.
yambukiensis Clastrier, 1987: 426. Zaïre.

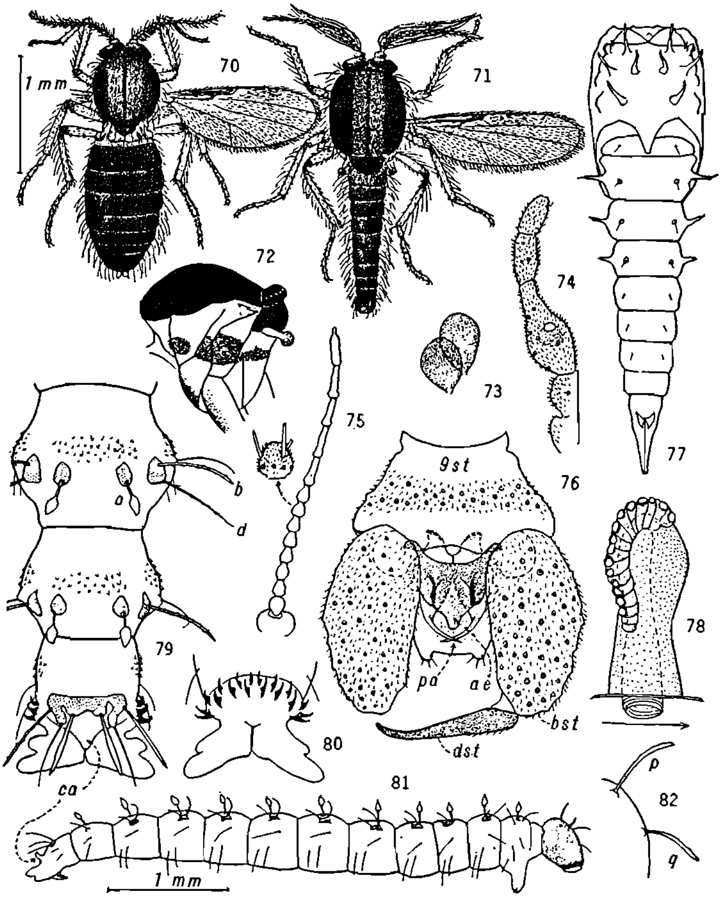
Genus *Forcipomyia* Meigen

Synonymy under subgeneric headings.

References: Saunders, 1924: 164 (larval morphology); Ingram & Macfie, 1924*a*: 378, 1924*b*: 523 (Afrotropical species); Saunders, 1956: 657 (revision of subgenera based on all stages); Dessart, 1963: 1 (monograph of Afrotropical species); Wirth & Ratanaworabhan, 1978: 493 (key to subgenera); Debenham, 1987*a–d*: 35 (taxonomic discussion; key to subgenera; revision Australasian species).

Diagnosis: Small to moderately large species, wing length 1–4 mm. Body short, stout, and very setaceous (Figs 70–71); often with flattened, striated scales. Eyes bare. Mesonotum without humeral pits, with dense setae, and with scattered longer bristles. Abdomen and legs with long bristles, especially in ♂. Femora unarmed; empodium well developed (absent in ♂ of *Phytohelea*); claws strongly curved, usually slender. Wing (Figs 70, 116) broad; surface with dense appressed macrotrichia and fine microtrichia; costa to middle of wing or beyond; first radial cell narrow and almost or completely obliterated, second small but distinct, tip of vein R4 + 5 nearly always curved up to costa and not sharply angled; crossvein r–m very oblique; squama with a tuft of setae. ♀ abdomen (Fig. 70) short and stout, bluntly rounded caudally; one or two spermathecae. ♂ genitalia not inverted; aedeagus (Fig. 76) usually shield-shaped; parameres usually present, of variable shapes (Fig. 83).

Immature stages: Larvae diverse (Fig. 83); usually with elongated, segmented body, with simple or variably modified setae and tubercles. Head (Fig. 95) usually hypognathous. Head and body with definite setation (setae with letter designation proposed by Saunders, 1924) (Figs 95–97); *p* setae of head present in *Forcipomyia s. s.* complex, absent in *Thyridomyia* complex; *a* setae of body spear-shaped in *Forcipomyia* complex, not in *Thyridomyia* complex. Last segment usually with distinct median projection or cauda (Fig. 97). Pupa (Fig. 77) with or without larval exuviae attached to posterior segments; prothoracic respiratory horn



Figs 70–82. *Forcipomyia genualis* (Loew): 70, female; 71, male; 72, female thorax, pleural pigmentation; 73, female spermathecae; 74, female palpus; 75, female antenna; 76, male genitalia; 77, pupa; 78, pupal respiratory horn; 79, larva, last 3 segments; 80, larva, anal pseudopod; 81, larva; 82, larval head setae.

usually short and knob-like (Fig. 78), sometimes with basal swelling (Fig. 83); arrangement of terminal spiracular openings variable; body segments with variable setation, from short bristles to long fleshy processes or short setose swellings; setation of different segments not identical; terminal processes of last segment usually long and tapered, sometimes short; ♂ genital processes dorsal or ventral.

Biology: Diverse; see discussions under subgenera. Adults attracted to flowers and important in pollination of tropical crops such as *Hevea* rubber, cocoa, and avocado. Saunders (1959) discussed successful methods he devised for the collection, rearing and study of the immature stages of *Forcipomyia* midges, especially for the cocoa-pollinating species.

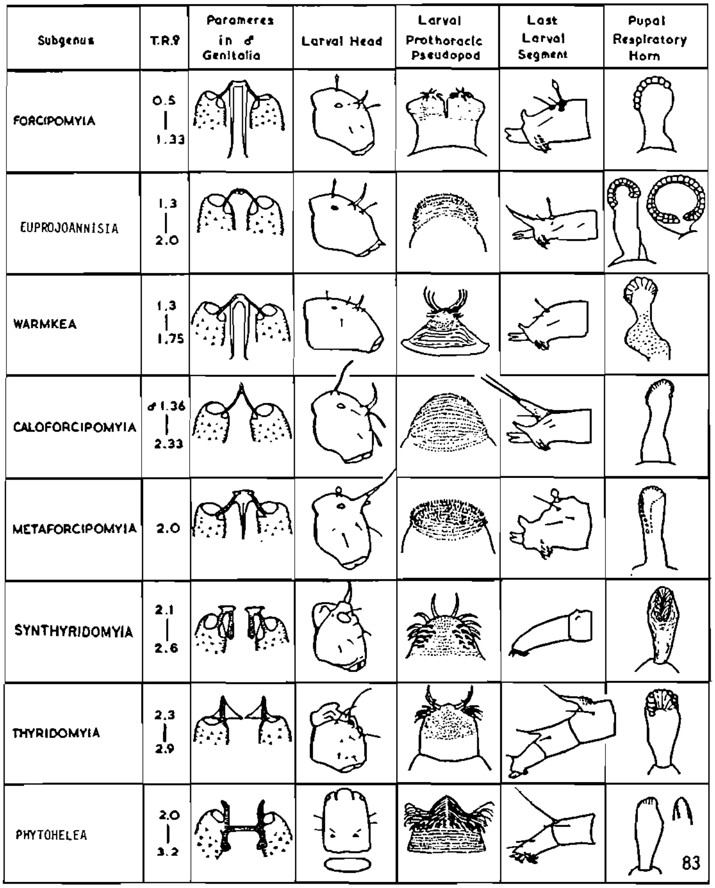


Fig. 83. Synoptic table of *Forcipomyia* subgenera (after Saunders 1956).

Subgenus *Caloforcipomyia* Saunders

(Figs 83, 109–110)

Forcipomyia, subgenus *Caloforcipomyia* Saunders, 1956: 680. Type species, *Forcipomyia caerulea* Saunders, by original designation.

Diagnosis: Usually with green or blue pigmentation in subcutaneous fat body persisting from larva. Antenna elongate, verticils long. Palpus (Fig. 109) slender; third segment with small sensory pit; fourth and fifth segments fused or not fused. Hind tarsal ratio 1,2–1,9. Claws and empodium well developed in both sexes. Wing often with conspicuous pattern of dark and pale scale-like macrotrichia; costal ratio well over 0,5; second radial cell open, elongate. Two spermathecae. ♂ genitalia (Figs 110) with basistylar apodemes joining to form an inverted V; aedeagus usually with distal process long and slender; parameres entirely absent.

Immature stages (after Saunders 1956): Larva with body not flattened, more elongate than usual for genus. Head strongly hypognathous with long, forward-curling p setae (Fig. 83). Prothoracic pseudopod a simple spinulose cushion. Last abdominal segment bearing a large dorsal chitinous process extending up and back beyond cauda and anal gills, with two basal and two long, terminal, stout setae. Cauda moderately long and pointed, without lateral fringe of setae; anal blood gills two, bifid; anal pseudopod normal. Pupa relatively spineless, with prominent pair of setigerous processes, conical at base, on dorsum of thorax just above and behind prothoracic respiratory horns. Respiratory horn slender, with row of spiracular openings across tip (Fig. 83). Larval exuviae retained on abdomen; terminal abdominal processes greatly attenuated in both sexes, ♂ sexual processes dorsal. Larvae on rotting wood in forest.

Distribution: Worldwide; 20 species.

Afrotropical species: The Afrotropical Catalogue lists 5 species; additions: *campanula* de Meillon & Downes, 1986: 142. South Africa.

Subgenus *Euprojoannisia* Brèthes

(Figs 83–101)

Euprojoannisia Brèthes, 1914: 155. Type species, *Euprojoannisia platensis* Brèthes, by original designation.

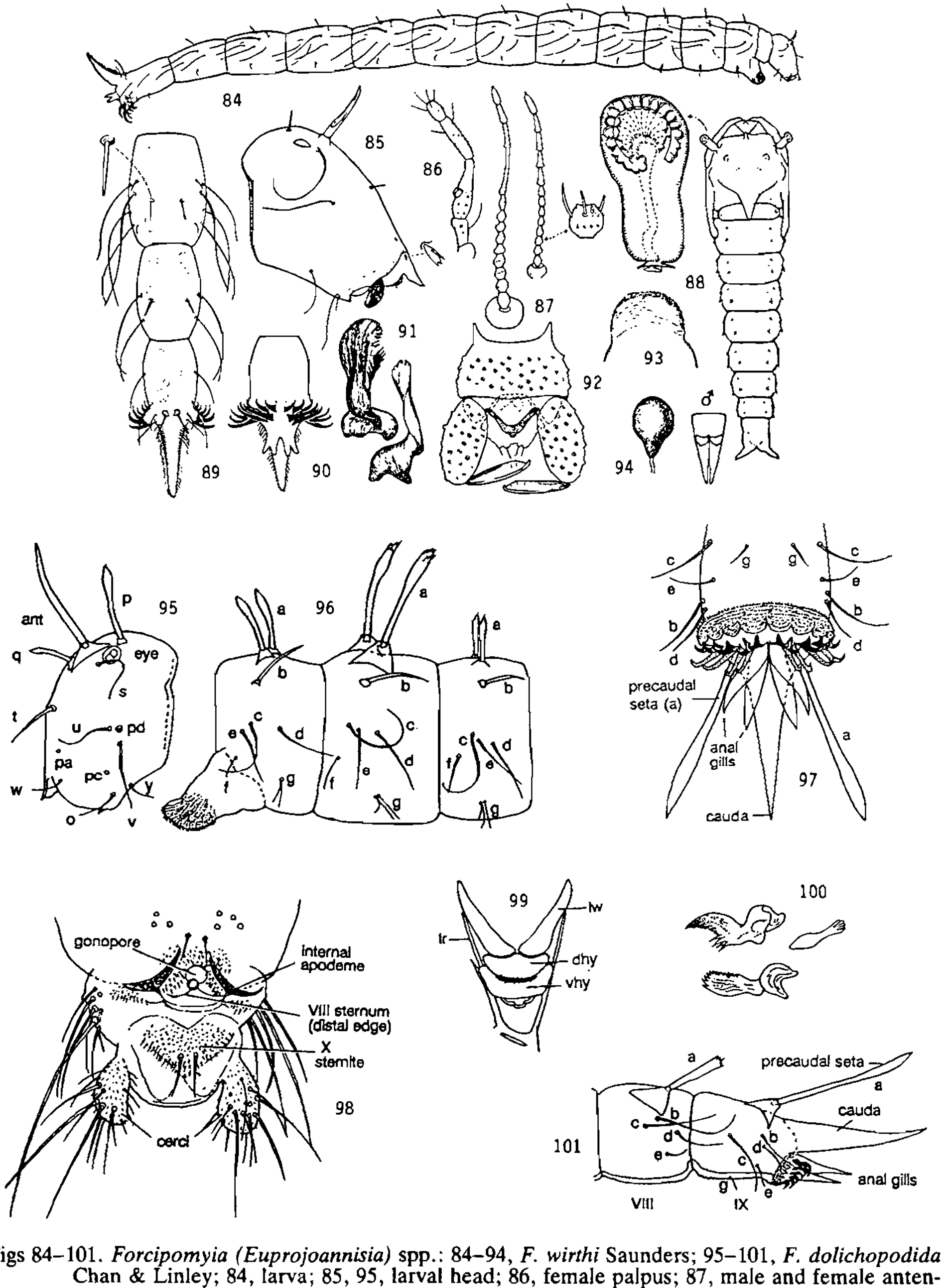
Euforcipomyia Malloch, 1915: 312. Type species, *Euforcipomyia hirtipennis* Malloch, by original designation.

Forcipomyia, subgenus *Proforcipomyia* Saunders, 1956: 662. Type species, *Forcipomyia wirthi* Saunders, by original designation.

References: Saunders, 1956: 662 (revision, immature stages); Bystrak & Wirth, 1978: 1 (diagnosis, biology; revision North American species); Debenham & Wirth, 1984: 851 (taxonomy; revision Australasian species).

Diagnosis: Small, unmarked, greyish brown midges; tarsal ratio 1,3–2,0. Palpus 5-segmented; fourth and fifth incompletely fused, the joint immovable (Fig. 86); third segment slender, with small round sensory pit. ♀ mandible usually with numerous fine teeth. Wing unmarked, densely setaceous with slender macrotrichia; costal ratio about 0,5. Legs often with numerous erect long bristly setae, especially on tibiae and proximal tarsomeres of hind leg; hind tibia with terminal spur often enlarged; posterior basitarsus often slightly expanded. Claws and empodium well developed in both sexes. One or two spermathecae. ♀ genitalia as in Fig. 98. ♂ genitalia (Fig. 92) usually rather short and stout; ninth tergum short; basistyle and dististyle usually stout; aedeagus of various shapes, usually a simple, low, triangular shield; basistylar apodemes joined in a slender arch; parameres only vestigial if present.

Immature stages (after Saunders 1956): Larva (Fig. 84) with head semi-hypognathous; head profile with two slight hollows or flat regions, not smoothly rounded; labrum with nose-like protuberance (Fig. 85); mandible (Figs 91, 100) broad apically, with right-angled twist, pharyngeal skeleton as in Fig. 99. Body often with faint reddish pigment pattern in subcutaneous fat body; body with *a* setae variable, often spear-shaped or spatulate, or borne on large tubercles (Fig. 96); prothoracic pseudopod (Fig. 93) a simple spinose cushion rarely



Figs 84–101. *Forcipomyia (Euprojoannisia)* spp.: 84–94, *F. wirthi* Saunders; 95–101, *F. dolichopodida* Chan & Linley; 84, larva; 85, 95, larval head; 86, female palpus; 87, male and female antennae; 88, pupa; 89, 101, larva, posterior segments; 90, larval posterior pseudopod; 91, 100, larval mandibles, various views; 92, male genitalia; 93, larval prothoracic pseudopod; 94, female spermatheca; 96, larva, thoracic segments; 97, larva, last segment; 98, female genitalia; 99, larval pharyngeal skeleton.

surmounted by a pair of papillae bearing longer hooklets; anal pseudopod (Figs 90, 97) a transverse ridge bearing two rows of hooklets, sometimes large and long; cauda (Figs 89, 97, 101) long, pointed, and fringed with setae. Pupa (Fig. 88) without large spine-like cuticular processes, rarely retaining larval exuviae; prothoracic respiratory horn variable in size and shape, always bearing a double palisade of spiracular openings in partial or complete circlet; ♂ sexual processes dorsal.

Biology: Adults commonly visit flowers and are important pollinators of cocoa and other tropical crop plants. Larval habitats are variable, usually semi-aquatic; at margin of hot mineral springs, in terrestrial bromeliads, on underside of banana leaves lying on ground, in leaf axils of various monocotyledonous plants, from under dead leaves on wet rock face, etc. Carter (1919) stated that *F. psilonota* (as *F. ingrami* Carter) larvae were predaceous on larvae of the mosquito *Aedes aegypti* (L.) in the laboratory in Accra, Ghana. The midge larvae lived on the sides of the container just above the water line and pulled to pieces any mosquito larva stranded on the water margin that remained motionless. 'Apparently their usual breeding places are rot-holes in trees, as I have found them immediately after moistening the debris scraped out of rot-holes in Flamboyant trees.' *Forcipomyia psilonota* has also been reared from pupae in rice fields and from plants of *Pistia stratiotes*.

Distribution: Worldwide; 72 species.

Afrotropical species: The Afrotropical Catalogue lists 4 species; additions and corrections:

aenigma de Meillon & Downes, 1986: 146. South Africa.
arcis de Meillon & Downes, 1986: 143. South Africa.
avocadonis de Meillon & Wirth, 1979*e*: 188. South Africa.
mopsus de Meillon & Hardy, 1954: 71. South Africa; Madagascar (from *Lasiohelea*).
soranus de Meillon, 1943: 103. South Africa (valid species).
tsacasi Clastrier, 1983*c*: 38. Seychelles.

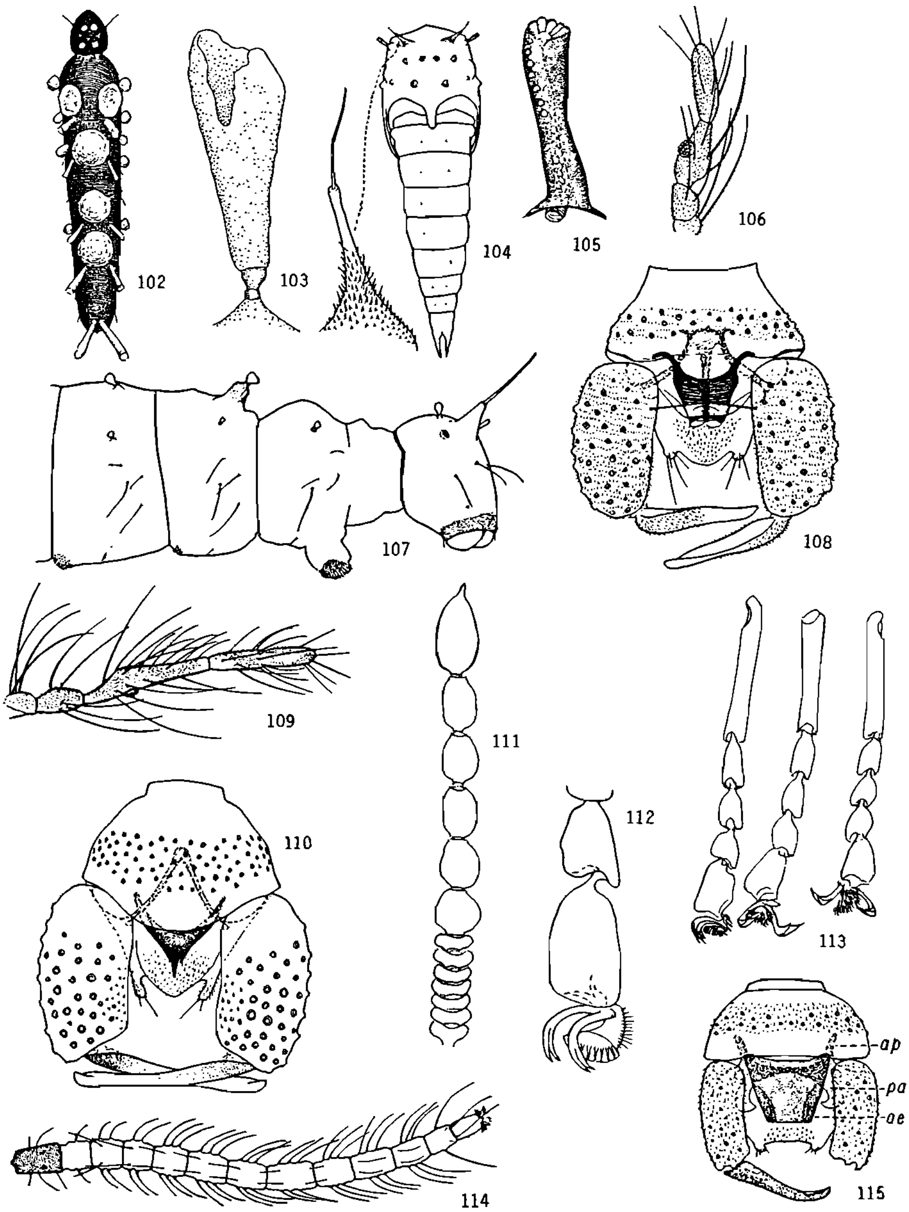
Subgenus *Forcipomyia* Meigen

(Figs 70–83)

Forcipomyia Meigen, 1818: 73, 75. Type species, *Tipula bipunctata* Linnaeus, by designation of Westwood, 1840: 126).

Reference: Dessart, 1963: 1 (revision of Afrotropical species; keys).

Diagnosis: Medium size midges (Figs 70–71); wing length usually 1–2 mm. Body with or without flattened striated scales, these usually not very broad. Hind tarsal ratio 0,5–1,3, usually about 1,0. ♀ antenna (Fig. 75) without marked increase in length of segments between 10 and 11, the segments usually short to long oval. Palpus (Fig. 74) 5-segmented, fourth and fifth without trace of fusion; third segment swollen proximally, with distinct sensory pit. ♀ mandible with or without fine teeth. Wing (Fig. 70) with dense macrotrichia, no bare areas along veins, frequently with setae forming colour pattern; costa usually reaching to about middle



Figs 102–115, *Forcipomyia* spp.: 102–108, *F. (Metaforcipomyia) cerifera* Saunders; 109–110, *F. (Caloforcipomyia) varicolor* Saunders; 111–112, *F. (Pterobosca) paludis* (Macfie); 113, *F. (P.) fusicornis* (Coquillett); 114–115, *F. (Phytohelea) caribbeana* Saunders; 102, larva with wax globules; 103, larva, dorsal wax chaeta; 104, pupa; 105, pupal respiratory horn; 106, 109, female palpus; 107, larva, head and thorax; 108, 110, 115, male genitalia; 111, female antenna; 112, female tarsomeres 4 and 5; 113, female tarsi; 114, larva.

of wing; first radial cell present or absent, second radial cell short. Tibiae of ♀ frequently with extensor row of modified hastate spines. Empodium and claws well developed in both sexes. Two spermathecae (Fig. 73) present. ♂ genitalia (Fig. 76) with diststyle not expanded apically; parameres well developed, separate distally, fused at base or connected by a basal bridge, basistylar apodemes slender.

Immature stages: Larva (Fig. 81) elongate, cylindrical, segmentally constricted, with numerous body chaetae rarely long; a dorsal pair frequently spear-shaped. Head hypognathous, profile smoothly rounded; antenna simple, moderately long, stout or tapered and rod-like with a small terminal papilla; p and *q* setae (Fig. 82) long, simple, and pectinate, spiculate, or hastate on a long stalk. Abdomen (Fig. 79) with *a* seta usually hastate on a slender stalk, sometimes rod-like or bulbous; *b*, *c*, and *d* setae usually simple and finely pectinate or spiculate, frequently on large basal tubercles, bases of *b* and *d* often fused; sometimes a chitinised bar joining the *a* setae dorsally on some segments. Prothoracic pseudopod (Fig. 83) apically cleft, with hooklets on each branch; anal pseudopod (Fig. 80) usually an undivided transverse ridge bearing two rows of hooklets, sometimes bilobed. Cauda (Fig. 79) absent or minute. Pupa (Fig. 77) with varying number of spines and cuticular processes; retaining larval exuviae on last 3–5 segments. Prothoracic respiratory horn (Fig. 78) of variable length, apex more or less swollen into a knob, with several to many spiracular openings in a curving or irregular row over apex and down the side. Terminal abdominal processes long and tapering; ♂ genital processes dorsal.

Biology: Females are attracted to flowers and are not known to suck vertebrate blood or insect haemolymph. Larvae are terrestrial and are usually found in groups of about 20–100 in rotting vegetable matter or under tree bark, where they feed on fungi, and to a lesser extent on the moist organic matter itself. The hastate *a*-setae of the larvae secrete droplets of a fluid that Hinton (1955) showed is repellent to ants. The larvae, when ready to pupate, assemble in a somewhat circular group with the heads inward, and on pupation the cast larval exuviae form a protective barrier repellent to predators. Known larval habitats of the Afrotropical species as follows:

F. ashantii Ingram & Macfie reared from rotting pseudostems of banana and from vegetable matter in rot hole of a tree; *F. biannulata* I. & M. from fallen fruit of a sausage tree; *F. castanea* (Walker) from banana stem and vegetable matter in a rot hole; *F. hirsuta* I. & M. from decaying banana fibre; *F. randensis* de Meillon from under bark of a dead gum tree and under bark of a dead pine stump; and *F. striaticornis* Kieffer from inside the stem of *Lobelia bequaertiana*.

Distribution: Worldwide; 297 species.

Afrotropical species: The Afrotropical Catalogue lists 41 species; additions:
creesi de Meillon, Meiswinkel & Wirth, 1982: 123. South Africa.
elegans de Meillon & Wirth, 1987*a*: 36. South Africa.
furfura de Meillon & Wirth, 1989*b*: 205. Zimbabwe.
guttata de Meillon & Wirth, 1989*b*: 204. Zimbabwe.
letebanus de Meillon, Meiswinkel & Wirth, 1982: 125. South Africa.

pulla de Meillon & Wirth, 1981*b*: 527. South Africa.
sensillata Clastrier, 1983*c*: 44. Seychelles.
vesicula de Meillon & Wirth, 1983*a*: 350. South Africa.

Note: Debenham (1987*d*) included *Forcipomyia hamoni* de Meillon (1959*a*: 329) in her new subgenus *Dycea*, otherwise containing only four Australasian and one Japanese species. The principal characters separating *Dycea* from *Forcipomyia s. s.* are the location of the palpal pit at or just past midlength of the third segment, the toothed mandibles in the female, and the characteristic shape of the ♂ parameres. Since only the ♂ is known of *hamoni*, it is here provisionally retained in *Forcipomyia s. s.* pending discovery of the female, and *Dycea* is not listed from the Afrotropical Region.

Subgenus *Lasiohelea* Kieffer

(Figs 83, 116–126)

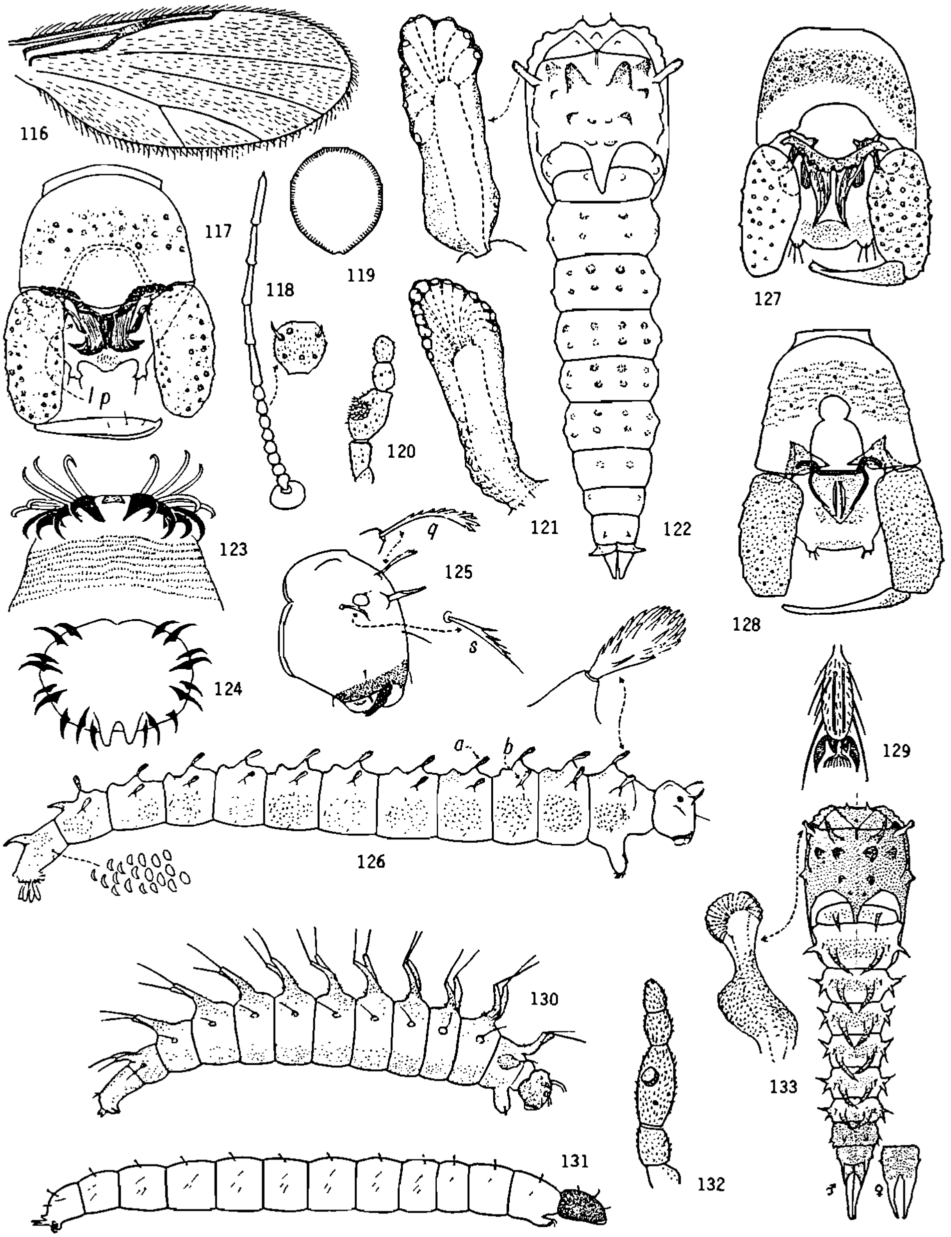
Lasiohelea Kieffer, 1921*a*: 115. Type species, *Atrichopogon pilosipennis* Kieffer [= *Ceratopogon velox* Winnertz], by original designation.

Parapterobosca Harant, Huttel & Huttel, 1951: 468. Type species, *Pterobosca anthropophila* Harant, Huttel & Huttel, by original designation.

References: Saunders, 1964: 463 (revision, all stages); Debenham, 1983: 1 (taxonomy; revision Australasian species).

Diagnosis: Small, unmarked, usually shining brownish to blackish species. ♀ antenna (Fig. 118) with proximal flagellar segments discoidal, subspherical or short oval; distal five segments (six in *F. anthropophila*) subcylindrical and much elongated. Palpus (Fig. 120) 5-segmented; third segment usually short and stout with sensory pit or scattered sensilla. ♀ mandible narrowly pointed, with numerous fine teeth. ♀ cibarium with armature of sharp spines. Empodium and claws well developed in both sexes; hind tarsal ratio usually between 1,0 and 3,0; tibial comb with 5–6 spines. Wing (Fig. 116) without colour pattern, with rather dense suberect macrotrichia, usually with bare lines along veins; costa extending distinctly beyond middle of wing; vein Rs closely paralleling costa causing second radial cell to appear long and narrow. One spermatheca (Fig. 119) without neck, the opening to the duct with large diameter (except in *F. anabaenae*). ♂ genitalia (Fig. 117) with ninth segment moderately short, basistyle usually slender, dististyle elongate, usually rather straight; aedeagus complicated, subdivided into pair of recurved sclerites, each bearing apical strong hook-like process; basistylar apodemes joined in a slender, ribbon-like basal arch (with membranous flange in *anabaenae*); parameres absent.

Immature stages (after Saunders, 1964): Larva (Fig. 126) orange brown in colour, rarely yellow, slender. Head (Fig. 125) dark, hypognathous, with four low prominences on vertex; antenna small, normal in form and position; *q* and *s* setae pectinate or simple; ocular setae present. Body with *a* setae torch-like (Fig. 126), variable in length, borne on variably prominent tubercles; *b* setae similar to *a* setae but smaller; paired horn-like tubercles or their rudiments on dorsum of last segment and sometimes on penultimate segment. Prothoracic pseudopod (Fig. 123) well developed, undivided, bearing four pairs of stout black hooklets and five pairs of slender hyaline hooklets; anal pseudopod (Fig. 124) armed with



Figs 116–133. *Forcipomyia* spp.: 116–120, 122–126, *F. (Lasiohelea) cornuta* Saunders; 121, *F. (Lasiohelea)* sp.; 127, *F. (Synthyridomyia) acidicola* (Tokunaga); 128, 130, *F. (Thyridomyia) monilicornis* (Coquillett); 129, 131, 133, *F. (Warmkea) bicolor* Saunders; 132, *F. (Trichohelea) crinita* Saunders; 116, female wing; 117, 127–128, male genitalia; 118, female antenna; 119, spermatheca; 120, 132, female palpus; 121, pupal respiratory horn; 122, 133, pupa; 123, larva, prothoracic pseudopod; 124, larva, caudal view of anal pseudopod; 125, larval head; 126, 130–131, larva; 129, female tarsomere 5.

nine pairs of hooklets in double ring practically surrounding end of body; cauda replaced by four low rounded tubercles across tip of last segment; cuticular armature scalelike. Pupa (Fig. 122) with orange or yellow subcutaneous colour persisting from larva; head with small tubercles on all three sclerites, the anterior pair setigerous; thorax with one pair of large dorsal tubercles, variable number of lesser tubercles, none setigerous; abdomen with many small tubercles; terminal sexual processes directed outwards, sharply pointed, effectively retaining larval exuviae, position ventral in ♂; prothoracic respiratory horn (Figs 121–122) narrow with posterior 'heel' usually distinct, 4–14 spiracular openings across tip of horn.

Biology: Females habitually suck vertebrate blood, usually daytime-biters. Larvae usually found on mossy rotting wood in deep shade; often on under side next to wet soil; also in moss or algae.

Distribution: Worldwide, mostly tropical; 88 species.

Afrotropical species: The Afrotropical Catalogue lists 9 species; additions and corrections:

latiunguis Clastrier, 1983*c*: 47. Seychelles.
montana de Meillon & Downes, 1986: 147. South Africa.
mopsus de Meillon & Hardy, 1954: 71. South Africa (to *Euprojoannisia*).
richardlanei Clastrier, 1983*c*: 50. Seychelles.

Subgenus *Lepidohelea* Kieffer

Lepidohelea Kieffer, 1917*b*: 364. Type species, *Ceratopogon chrysolophus* Kieffer, by original designation.

Reference: Debenham, 1987*c*: 309 (taxonomic discussion; revision Australasian species.

Diagnosis: Closely resembling species of *Forcipomyia s. s.* Body densely covered with striated, flattened scales, often grouped and distributed to form a complex colour pattern; wing and legs usually ornamented with pale and dark areas or bands. ♀ antenna moderately slender, last five segments not greatly elongated. Palpus 4- or 5-segmented; third segment slender with small sensory pit. Costa short, not reaching middle of wing. Hind tarsal ratio about 1,0. One or two spermathecae present. ♂ genitalia with well-developed, usually stout and variably ornamented parameres, usually not joined at bases, but attached to diagonal basistylar apodemes; ninth segment and basistyles short and stout; dististyles elongate, and often sinuate with distinct distal expansion.

Immature stages (After Debenham, 1987*d*): Larva with head hypognathous; antenna a simple tapered rod, *p* and *q* setae long, expanded near base but becoming filamentous. Prothoracic *a* seta swollen near base, then filamentous, remaining *a* setae rod-like with hastate apex, *b* setae similar to prothoracic *a* seta but larger and longer, other setae simple, a thin dorsal chitinised bar connecting the *a* setae on all abdominal segments. Prothoracic pseudopod apically cleft, with four small dark spines at apex of each branch; anal pseudopod cleft with each branch bearing 4–6 hooklets apically and 3–4 on inner lateral side. Cauda absent. Pupa pale; prothoracic respiratory horn small, with or without basal heel, with 7–10 spiracular openings extending down from apex. Thorax with seven pairs of long cuticular processes, some spinose apically; abdomen with similar processes and/or small spinose tubercles; terminal processes long and tapering; ♂ genital processes dorsal. Larval exuviae retained on distal abdominal segments.

Biology: De Meillon (1931: 335) described all stages of *F. randensis*, which was reared from a dead pine stump. Kaufmann (1975*a*) discussed the life history of *F. squamipennis* Ingram & Macfie, an important cocoa pollinator in Ghana. Larvae were cultured in the laboratory on moist, rotten, cocoa-pod husks. *F. venusta* I. & M. has been reared from rotting banana fibre.

Distribution: Worldwide; 36 species.

Afrotropical species: The Afrotropical Catalogue lists 7 species; additions and corrections:

chrysolopha Kieffer, 1911*b*: 333 (*Ceratopogon*). Seychelles. According to Clastrier (1983c) *F. chrysolopha* is confined to the Seychelles, and *F. lepidota* Ingram & Macfie is the correct name to be applied to the widespread Afrotropical species.

hastata de Meillon & Wirth, 1981*c*: 565. South Africa, Zimbabwe.

ikinae de Meillon, Meiswinkel & Wirth, 1982: 127. South Africa.

lepidota Ingram & Macfie, 1924*b*: 566. Ghana; Afrotropical and Oriental Regions.

randensis de Meillon, 1931: 335. South Africa.

roseae de Meillon, Meiswinkel & Wirth, 1982: 129. South Africa.

Subgenus *Metaforcipomyia* Saunders

(Figs 83, 102–108)

Forcipomyia, subgenus *Metaforcipomyia* Saunders, 1956: 685. Type species, *Forcipomyia cerifera* Saunders, by original designation.

Diagnosis: Small midges with striated, scale-like setae. ♀ antenna with basal flagellar segments flask-shaped; five distal segments very little elongated. Palpus (Fig. 106) 4-segmented, fourth and fifth fused inseparably; third segment with sensilla borne in circumscribed cluster resembling a shallow pit. Costa scarcely reaching to middle of wing; first radial cell narrowly open; second open, short; vein M2 absent. Hind tarsal ratio about 2,0; claws and empodium well developed in both sexes. Two spermathecae present. ♂ genitalia (Fig. 108) with curved basistylar apodemes joined in angular, anterodirected arch, parameres fused in midline and extending caudad to tip of aedeagus.

Immature stages (after Saunders, 1956): Larva (Fig. 102) not flattened, general form as in subgenus *Forcipomyia*; head hypognathous, antenna situated on bases like those of many *Atrichopogon* larvae. Prothoracic pseudopod a coarsely spinose cushion; anal pseudopod normal; cauda short, lobose. Head and body with knob-like chaetae (Fig. 107) bearing tubes and cones (Fig. 103) of white wax and globules powdered with wax (Figs 102). Pupa (Fig. 104) practically devoid of setae; thorax with anterior pair of slender, spinulose, setigerous processes and four other low spinulose processes; prothoracic respiratory horn (Fig. 105) slender, with row of spiracular openings over top and halfway down stem; larval exuviae retained.

Biology (Saunders 1956): Larvae occur under rotting wood on the forest floor, the wax bodies creating a resemblance of the larvae to pieces of wood covered with fungus spore-bodies.

Distribution: Worldwide; 12 species.

Afrotropical species:
hesiones de Meillon, 1936: 167. South Africa.
stewarti de Meillon & Downes, 1986: 149. South Africa.

Subgenus *Microhelea* Kieffer

Microhelea Kieffer, 1917*b*: 364. Type species, *Atrichopogon microtoma* Kieffer (designation of Kieffer, 1921*b*: 7, with explanatory annotation on erroneous designation in 1917 work).

References: Wirth, 1971: 231 (revision; diagnosis; phasmid parasites); Wirth, 1972: 564 (diagnosis; synonymy; revision of caterpillar parasites of the Neotropical Region).

Diagnosis: Size large for *Forcipomyia*, wing length 1,5–2,0 mm. Wing without pale spots, densely clothed with dark brown decumbent macrotrichia; numerous dark, long, slender, striated scales on costa and radial field; costal ratio about 0,50; first radial cell obsolete, second with distinct lumen. ♀ antenna with proximal flagellar segments globular to short oval, distal five segments elongate. Palpus quite characteristic, 5-segmented, third segment in ♀ broadly inflated to well past middle, sometimes nearly to tip, with sensory pit quite deep, extending nearly to base of segment, opening toward apex of segment by a small round pore, surface of segment near pore with a number of slender, peglike, hyaline sensory spines; fourth segment longer than fifth, usually much longer. Proboscis well developed, with expanded labella in phasmid parasites, slender apically in caterpillar parasites. ♀ mandible with distinct teeth, numerous and minute in caterpillar parasites, but fewer and stronger in phasmid parasites. Maxilla with minute lateral teeth in caterpillar parasites and stout blunt teeth or corrugations in phasmid parasites. Legs with numerous long setae and slender striated scales; basitarsi usually about half the length of second tarsomere. Empodium well developed in both sexes. Two spermathecae present. ♂ genitalia similar to those of *Forcipomyia s. s.*; parameres forklike, fused proximally to half or more of total length, the distal prongs pointed.

Immature stages (after Chan & LeRoux 1971*a*: 743, *F. intonsa*): Larva with principal setae of head and dorsum with minute spinules; *a* setae short and spear-shaped. Pupa without tubercles on abdominal segments; prothoracic respiratory horn small, club-shaped, bearing 16–22 spiracular openings curving up back and over top in an S-shape. Otherwise as in subgenus *Forcipomyia*.

Biology: Adult females suck haemolymph from stick insects (Phasmidae), katydids, caterpillars and sawfly larvae. Larvae have been reared from wood around a stagnant pool; from mosses, liverworts, and algae on a clay bank; from animal droppings, vegetable debris, damp underwood, and from under tree bark. Ingram & Macfie (1924*a*) described the larvae of *F. inornatipennis* reared from eggs deposited by a female in the laboratory. Kaufmann (1974*b*) described the life history of *F. inornatipennis* in Ghana, where it is an important pollinator of cocoa. Larvae were cultured in the laboratory on cocoa husks, banana stems, goat manure, and/or other decayed vegetable matter.

Distribution: Worldwide; 33 species.

Afrotropical species:

fuliginosa Meigen, 1818: 86 (*Ceratopogon*). Germany; cosmopolitan; common parasite of caterpillars and sawfly larvae).

inornatipennis Austen, 1912: 107 (*Ceratopogon*). Nigeria; Afrotropical Africa.

Subgenus *Pedilohelea* de Meillon & Wirth

Forcipomyia, subgenus *Pedilohelea* de Meillon & Wirth, 1980: 9. Type species, *Forcipomyia clastrieri* Dessart, by original designation.

Reference: De Meillon & Wirth, 1980: 9 (world revision).

Diagnosis: Small midges (wing length 0,7–1,3 mm) without any distinctive markings. Antennal verticils of ♀ long and stiff; flagellar segments comparatively elongate, antennal ratio 0,9–1,3. Palpus 4-segmented; third segment with rudimentary or shallow, poorly marked sensory pit. ♀ mandible without teeth. Tarsal ratios usually less than 0,7 on all legs; hind tibial comb poorly developed; tarsomeres 1 and 2 of fore leg each with ventral row of short, strong, black spines, apical dark spines also present on some of remaining tarsomeres. Claws small, abruptly bent in middle and expanded spear-shaped distally, resembling those of subgenus *Warmkea*.

Wing without ornamentation; costa short, costal ratio 0,39–0,47. Halter usually infuscated. Body with abundant, narrow, 1–4 striated, scale-like setae, especially on costa and radial veins of wing. Two subequal spermathecae, usually without necks. ♂ genitalia with parameres broadly joined basally and more or less blade-like distally.

Immature stages and Biology: Unknown.

Distribution: Pantropical; 14 species.

Afrotropical species:

brevitarsata Clastrier, 1959*a*: 345 (*Lepidohelea*). Senegal. Preoccupied in *Forcipomyia* by *Lasiohelea brevitarsata* Ingram & Macfie, 1924*a*. Synonym of *F. clastrieri* Dessart.

brincki de Meillon, 1959*a*: 328. South Africa.

clastrieri Dessart, 1963: 183. Replacement name for *brevitarsata* (Clastrier). Senegal; Ghana, Nigeria, Saõ Tomé).

draconis de Meillon & Wirth, 1980: 17. South Africa.

eshowensis de Meillon, 1937: 361. South Africa.

haroldi de Meillon & Wirth, 1989*b*: 208. South Africa.

Subgenus *Phytohelea* Remm

(Figs 83, 114–115)

Forcipomyia, subgenus *Phytohelea* Remm, 1971: 189. Type species, *Ceratopogon bromelicola* Lutz, by original designation.

Apelma Kieffer (misident.) of authors.

Reference: De Meillon & Wirth, 1979*e*: 178 (world revision; keys).

Diagnosis: Small, pale-bodied, unmarked midges; wing length about 1,0 mm. Basal flagellar segments of ♀ compressed, as many as four segments absent in some species. Palpus 5-segmented; fourth and fifth segments not fused; third segment with definite sensory pit. ♀ mandible with numerous small teeth. Empodium present in ♀; present, absent, or vestigial in ♂. ♀ claws slender, curved, and distally pointed. Wing with sparse macrotrichia, iridescent, unmarked; costa ending at or near middle of wing; second radial cell open, longer than in subgenus *Forcipomyia*. Spermathecae two. ♂ genitalia (Fig. 115) with ninth sternum short and broad; aedeagus variably shield-shaped; parameres spatulate, joined by stout crossbar, extending back from forward-projecting basistylar apodemes, the complex appearing as a stout H-shaped structure in ventral view.

Immature stages: Larva (Fig. 114) with head flattened, prognathous, roughly rectangular in dorsoventral view; antenna reduced to circular windows on front corners of head. Body elongate, vermiform, dorsoventrally flattened, with many fine lateral setae often 'finned,' few dorsal setae; a characteristic dorsal pair of setae arising from sclerotised crossbar on posterior margin of penultimate segment; prothoracic pseudopod conical, bearing many curved hair-like hooklets beyond a row of short, stout hooks; anal pseudopod a transverse row of 10 black thorn-like hooks and a second row of eight slender hyaline hooklets, the outermost usually stouter and serrate on inner surface; body ending in a dorsal, median, bluntly conical point not turning up but still to be regarded as a cauda; two pairs of anal papillae, bifurcate, fine-pointed; cuticle devoid of armature. Pupa elongate, agile, never retaining larval exuviae; setae few to none on thorax, numerous spines and short setae on sides of abdomen; prothoracic respiratory horn small with narrow base, a U-shaped row of spiracular openings at tip; terminal processes widely spaced, short, with small seta on outer surface; genital processes of ♂ ventral.

Biology: Larvae are found living submerged in water in leaf axils of water-holding plants such as *Dracaena*, *Pandanus*, *Colocasia*, *Cordyline*, bromeliads, etc. The pupa sheds the larval skin completely and leads an active submerged life until the imago is ready to emerge, when vigorous writhing motions bring it up out of the water. *Forcipomyia bacoti* has been reared from a tree hole in Zululand, a hole in a tree fern, and leaf axils of *Dracaena*, *Musa*, pineapple and lily. *F. tzaneenensis* was reared from the leaf axils of *Colocasia*.

Distribution: Pantropical; 22 species.

Afrotropical species: The Afrotropical Catalogue lists 2 species; additions and corrections:

bacoti Ingram & Macfie, 1923: 55 (*Apelma*). Sierra Leone; Ghana, South Africa, Uganda.

natalia de Meillon, 1936: 158 (*Lasiohelea*). South Africa. Synonym of *bacoti* (Ingram & Macfie).

tzaneenensis de Meillon & Wirth, 1979*e*: 184. South Africa; Ghana.

Subgenus *Pterobosca* Macfie

(Figs 111–113)

Pterobosca Macfie, 1932: 266. Type species, *Ceratopogon aeschnosuga* de Meijere, by designation of Macfie, 1940*a*: 16.

References: Tokunaga & Murachi, 1959: 229 (key to species); Wirth & Ratanaworabhan, 1976: 241 (taxonomy, habits; immature stages).

Diagnosis: Moderately small, unmarked, dark brown midges. ♀ antenna (Fig. 111) with distal six or seven flagellar segments elongate (normally five elongate distal segments in family); proximal segments discoidal or subspherical. Palpus 5-segmented, usually short and stout; third segment stout with distinct round pit. ♀ mandible stout, apex round and provided with 10–15 strong teeth. Empodium (Figs 112–113) of ♀ large and modified in a complex clinging disc; claws present or absent; hind tarsal ratio 3,0 or more. Wing with costa moderately long, extending slightly past middle of wing; first radial cell slit-like or almost closed; second radial cell usually open, sometimes obliterated; macrotrichia moderately dense, usually with bare lines bordering veins. One or two spermathecae. ♂ genitalia with ninth tergum moderately large with rounded posterior margin; basistyle and dististyle elongate and moderately slender; aedeagus with posterior margin rounded and bearing a submedian pair of distally pointed, dorsoposterior processes; parameres joined in midportion in an H-shaped structure, the posterior arms of the H moderately stout.

Immature stages (Wirth & Ratanaworabhan, 1976: 241; presumed immature stages of *F. hutsoni*): Larva long, vermiform, dorsoventrally flattened, very similar to larva of *Phytohelea*. Head prognathous, more rounded in profile than in *Phytohelea*; body segments with setae inconspicuous, nearly bare; penultimate body segment with a moderately elevated, biramous, transverse process, the ends of which are drawn out in a pair of yellowish, long, tapering, dorsally directed processes; anterior and posterior pseudopods well developed, entire, similar to those of *Phytohelea*. Pupa elongate, not retaining larval exuviae; without setae, but abdomen with three pairs of small subconical tubercles on each segment; prothoracic respiratory horn relatively long and slender, slightly expanded distally with a curved row of about 10 spiracular openings at tip, surface smooth.

Biology: Females are adapted for clinging to wings of larger insects, usually Odonata or Chrysopidae, and sucking haemolymph from the basal wing veins. The presumed larvae of *Forcipomyia hutsoni* were taken from leaf axils of *Pandanus*.

Distribution: Worldwide, mostly tropical; 19 species.

Afrotropical species:

hutsoni Wirth & Ratanaworabhan, 1976: 242. Aldabra Atoll.
mollipes Macfie, 1932: 272 (*Pterobosca*). Liberia.
paludis Macfie, 1936: 63 (*Pterobosca*). England; Europe, Uganda.
pinheyi Clastrier & Legrand, 1984: 174. Mauritius.

Subgenus *Rhinohelea* de Meillon & Wirth

Forcipomyia, subgenus *Rhinohelea* de Meillon & Wirth, 1979*d*: 881. Type species, *Forcipomyia briani* de Meillon & Wirth, by original designation.

Diagnosis: Medium size, uniformly blackish setaceous midges; wing length 0,9–1,4 mm. Antenna moderately elongated, antennal ratio less than 1,0. Palpus 5-segmented; third segment with well-formed, deep sensory pit. Proboscis unusually long, as long or slightly shorter than fore femur; ♀ mandible slender with strong teeth. Legs with abundant fine setae, spines or scales absent; hind tarsal ratio 2,0 or more; claws slender, empodium well developed in both sexes. Wing without colour pattern and without broad scales, macrotrichia abundant; second radial cell open and elongate as in *Atrichopogon*; costal ratio 0,56 in ♀, 0,52 in ♂. ♀ with one dark pear-shaped spermatheca. ♂ genitalia with elongate ninth sternum, deep caudomedian excavation; ninth tergum short; basistyle short and simple; dististyle short, straight and stout, with tuft of long setae dorsally at base; aedeagus consisting of a strong, highly pigmented sclerite on each side of a median membranous part which is split down the middle, forming an inverted V. Parameres a pair of large sclerites joined basally, each with a large pointed tooth distally; a narrow sclerotised band joining base of each basistyle between aedeagus and parameres.

Immature stages: Unknown.

Biology: Adults of *F. briani* were collected from *Erica* heath in the southwest Cape Province, along with other Diptera with elongated mouthparts, presumably adapted for feeding in the deep tubular flowers.

Distribution: South Africa; 2 species.

Afrotropical species:
briani de Meillon & Wirth, 1979*d*: 882. South Africa.
khoisana de Meillon & Wirth, 1979*d*: 885a. South Africa.

Subgenus *Saliohelea* Wirth & Ratanaworabhan

Forcipomyia, subgenus *Saliohelea* Wirth & Ratanaworabhan, 1978: 494. Type-species, *Forcipomyia leei* Wirth & Ratanaworabhan, by original designation.

Diagnosis: Small, unmarked yellowish to brownish midges very similar to *Euprojoannisia*; wing length 0,62–0,83 mm. Palpus 4-segmented, fourth and fifth segments fused without trace of articulation, tapering to slender tip; third segment with or without sensory pit. Mandibular teeth absent. Body, wings, and legs usually more or less clothed with elongate, slender, scale-like setae with 1–3 striations. Wing unmarked; costa short, costal ratio 0,41–0,52 in ♀. Hind tarsal ratio 1,7–2,7; ♂ hind basitarsus sometimes expanded dorsally. Empodium well developed in both sexes; claws slender and curved. ♀ with one small functional spermatheca, usually tapering to slender neck, a minute vestigial second spermatheca also usually present. ♂ genitalia similar to those of *Euprojoannisia* or *Warmkea*. Ninth sternum transverse distally, with long slender anterolateral projections; basistyle moderately stout, dististyle long and slender. Aedeagus variable, usually with triangular basal portion without well-developed basal arch or lateral arms, this portion usually with distinct marginal sclerotisation; slender distal median process usually present, rounded or peglike. Parameres with basistylar apodemes forming a more or less V-shaped basal arch, with distinct mesal connective which is usually plate-like but may be narrow; a pair of submedian posterior sclerotised processes present or absent.

Immature stages: Larva unknown. Pupa with slender respiratory horn bearing six spiracular openings spaced loosely around apical margin giving it a crinite appearance.

Biology: *Forcipomyia leei* Wirth & Ratanaworabhan was reared from beneath bark of a fallen tree in the forest in Brazil.

Distribution: Pantropical; 5 species.

Afrotropical species:
brevicosta Clastrier, 1960*b*: 520 (*Lasiohelea*). Rep. Congo.
stami Wirth & Ratanaworabhan, 1978: 502. Zaïre.

Subgenus *Schizoforcipomyia* Chan & LeRoux

Forcipomyia, subgenus *Schizoforcipomyia* Chan & LeRoux, 1971*a*: 271. Type species, *Forcipomyia petersoni* Chan & LeRoux by original designation = *borbonica* Clastrier.

Reference: De Meillon, Meiswinkel & Wirth, 1982: 133 (key to Afrotropical species).

Diagnosis: Very similar to *Forcipomyia s. s.* and *Lepidohelea*. Antenna moderately long, antennal ratio about 1,0. Palpus 5-segmented; third segment moderately swollen with distinct, deep sensory pit. Wing usually with pattern of dark and light macrotrichia and flattened scale-like macrotrichia; costal ratio about 0,6; first radial cell completely obliterated, second small and moderately wide. Tibiae without hastate setae on extensor side; hind tarsal ratio about 1,0. Two ovoid spermathecae with short necks. ♂ genitalia with ninth segment, basistyles and dististyles short and stout; aedeagus V-shaped, bearing a pair of small sharp processes at tip; parameres with basal apodemes forming an arch with anterior apex truncate, bearing a pair of slender rods appressed to sides of aedeagus.

Immature stages (after Chan & LeRoux, 1971*a*): Larva similar to that of *Forcipomyia s. s.*; head hypognathous, *p* and *q* setae almost as long as head length, *s* setae absent; antenna with filament longer and more pointed than in *Forcipomyia s. s.*; body setae numerous, moderately long; *a* setae spear-shaped, not so rounded as in *Forcipomyia s. s.*; *b* setae long, thickened basally; prothoracic pseudopod medially divided, each half again unequally and indistinctly subdivided, the larger outer quarter bearing a crown of hooklets on apex; anal pseudopod bilobed, each lobe bearing eight hooklets; anal blood gills four, outer pair unequally bilobed; cauda small, bluntly conical. Pupa spiny with many moderately long tubercles, most bearing a short seta at apex; larval exuviae retained on last few segments; prothoracic respiratory horn thumb-shaped, short, with about 12 spiracular openings curving across apex and posterior margin; ♂ sexual processes small, dorsal.

Biology: Larvae of *Forcipomyia borbonica* Clastrier were found between bark and wood of a decaying tree in Singapore (Chan & LeRoux, 1971*a*).

Distribution: Worldwide, mainly tropical; 9 species.

Afrotropical species:
anna de Meillon, 1959: 331. South Africa.
borbonica Clastrier, 1959*b*: 436. Réunion; Seychelles, India, Singapore, Pacific Islands.
lecordeurorum de Meillon, Meiswinkel & Wirth, 1982: 132. South Africa.
rudebecki de Meillon, 1959*a*: 330. South Africa.
warreni de Meillon & Wirth, 1981*b*: 528. South Africa.

Subgenus *Synthyridomyia* Saunders

(Figs 83, 127)

Forcipomyia, subgenus *Synthyridomyia* Saunders, 1956: 688. Type species, *Lasiohelea acidicola* Saunders, by original designation.

Reference: Saunders, 1956: 688 (diagnosis; immature stages; habits).

Diagnosis: Similar to *Thyridomyia*; small unicolorous brown midges; wing length 0,5–1,1 mm. ♀ antennal segments subspherical basally, gradually increasing in length distad. Palpus 5-segmented; third segment with deep pit or with surface group of capitate sensilla. Hind basitarsus elongate, tarsal ratio 2,1–2,6; empodium well developed in both sexes. Wing without colour pattern, moderately clothed with macrotrichia, no scales; costa ending about middle of wing; second radial cell with distinct lumen. One spermatheca. ♂ genitalia (Fig. 127) with ninth sternum sometimes emarginate, but never like the deep 'window' of some *Thyridomyia*; ninth tergum rounded caudad; parameres in form of club- or rod-shaped posterior processes extending backward from variably shaped basistylar apodemes.

Immature stages (after Saunders 1956): Larva similar to that of *Thyridomyia*, but antenna elongate; with large basal tubercles placed high on frons; vertex with paired blunt tubercles; frons wrinkled; *p* and *q* setae absent. Prothoracic pseudopod large, undivided, bearing distally many slender and stouter hooklets arranged in several rows; posterior pseudopod a transverse ridge bearing two rows of black hooklets. Body segments with small dorsal and dorsolateral rounded tubercles bearing minute multiple setae; no *a* setae or long setae. Pupa with small tubercles present on head, thorax and abdomen; no long setae. Prothoracic respiratory organ slender, slightly enlarged distally, bearing an ellipse of spiracular openings with roots meeting centrally in a deep fissure. ♂ genital processes ventral. Larval exuviae not retained on tail of pupa.

Biology: Adults have been taken frequently at flowers, especially those of Umbelliferae. Tokunaga (1937*b*) took the larva of *F. acidicola* among wet stones on the shore of a volcanic lake which had an extreme acidity of pH 1,4 in Japan. Saunders (1956) collected larvae of *F. colemani* Wirth by Berlese funnel extraction from moss in Canada.

Distribution: Worldwide; 20 species.

Afrotropical species:
corsoni Macfie, 1926: 355. Tanzania.
exigua Ingram & Macfie, 1924*b*: 587. Ghana.
murina Winnertz, 1852: 26 (*Ceratopogon*). Europe; Holarctic, Afrotropical.

Subgenus *Thyridomyia* Saunders

(Figs 83, 128, 130)

Thyridomyia Saunders, 1925: 268. Type species, *Thyridomyia palustris* Saunders [= *monilicornis* (Coquillett)], by original designation.

Reference: De Meillon & Wirth, 1981*c*: 568 (key to Afrotropical species; synonymy).

Diagnosis: Small, uniformly brownish midges with unmarked wings; wing length 0,54–0,75 mm. ♀ antenna with proximal segments subspherical to slightly transverse, segments 11–15 moderately elongated. Palpus 5-segmented; third segment not greatly swollen. ♀ mandible slender and pointed, with 20–30 minute teeth. Hind basitarsus elongated, tarsal ratio 1,7–3,6; empodium well developed in both sexes; ♀ claws moderately strong and curved, simple. Wing short and broad in ♀; clothed with unflattened macrotrichia which are sometimes sparse or setiform; costa reaching beyond middle of wing; first radial cell closed or slitlike; second open, sometimes elongate, usually with oblique tip. ♀ genital sclerotisation usually distinctive, well developed; one spermatheca with distinct sclerotised neck. ♂ genitalia (Fig. 128) with elongate ninth segment bearing on the sternum a deep membranous 'window' or sometimes a poorly-developed caudomedian excavation; ninth tergum rounded. Basistylar apodemes usually triangularly expanded towards anterior end and bearing slender mesal connectives; no backward-directed parameres present. Aedeagus variable, usually with curved lateral sclerites and narrow submedian processes.

Immature stages (after Saunders 1956): Larva (Fig. 130) orange in colour. Head hypognathous; eyes comparatively large; antenna located at front of head, reduced to a flat disc on low basal ring or tubercle which is flanked by extremely reduced flagellum in the membrane outside the disc; vertex with 2–3 rounded swellings. Body segments variably provided with prominent setigerous processes or with small low tubercles bearing microscopic multiple setae, but no spear setae or *a* setae; cauda absent. Pupa with only small tubercles; prothoracic respiratory organ broad distally with narrow base; multiple spiracular openings in row across tip; ♂ genital processes ventral; larval skin not retained on tail of pupa.

Biology: Adults of both sexes can be found, sometimes in large numbers, on flowers; tropical species are pollinators of *Hevea* and *Theobroma*. Larvae are common on moss or moss-covered wood or rocks; some species breed in sap flows from tree wounds, or in decaying plant materials. The orange larvae are easily extracted from moss or other breeding material by Berlese funnel, and can be reared on the host material in vials or other small containers. In Ghana, *F. inconspicuosa* (Ingram & Macfie) was reared from a hollow in a kapok tree (*Ceiba*) (Ingram & Macfie 1924*b*).

Distribution: Worldwide; 42 species.

Afrotropical species: The Afrotropical Catalogue lists 7 species; additions:
gokwe de Meillon & Wirth, 1989*b*: 209. Zimbabwe.
watshami de Meillon & Wirth, 1989*b*: 210. Zimbabwe.

Subgenus *Trichohelea* Goetghebuer

(Fig. 132)

Apelma Kieffer, 1919: 64. Type species, *Apelma auronitens* Kieffer, by designation of Macfie, 1940: 16. Junior homonym, preoccupied by *Apelma* Billberg 1820.
Trichohelea Goetghebuer, 1920: 39. Type species, *Trichohelea tonnoiri* Goetghebuer [= *Apelma auronitens* Kieffer], by original designation.
Reference: Saunders, 1964: 473 (diagnosis, all stages).

Diagnosis: Small, stout, uniformly brownish midges. ♀ antenna with proximal flagellar segments transverse to spherical, much shorter than last five segments. Palpus (Figs 132) 5-segmented, short and stout; third segment not greatly swollen, usually with definite sensory pit. Proboscis stout, apex broad with well-developed fleshy lobes or fringing setae. Mandible well developed, apex usually broad with strong distal teeth, shape diagnostic for species; maxilla with lacinia variably provided distally with small teeth or transverse ridges. Wing unmarked, densely setaceous with slender decumbent macrotrichia; costa to slightly beyond middle of wing. Legs unbanded, hind tarsal ratio usually greater than 2,4; ♀ empodium well developed, ♂ empodium vestigial; ♀ claws variable, characteristic of each species. ♀ with two spermathecae with distinct necks. ♂ aedeagus shape variable, usually a low basal arch and low rounded hyaline posterior lobe with a slender peg-like distomedian process on dorsal side; parameres forming a U-shaped structure with broad clavate posterior lobes.

Immature stages (after Saunders 1964): Larva with head small, strongly hypognathous, depressed under prominent prothorax; prothorax with two pairs of large, hook-tipped setae on long, slender tubercles; *a* setae lacking; all body segments except last with small lateral tubercles bearing complex rosette setae; prothoracic pseudopod undivided; cauda absent. Pupa with well-developed tubercles on median sclerite of head, small to rudimentary on thorax and abdomen; prothoracic respiratory horn variable in shape and arrangement of spiracular openings; terminal sexual processes dorsal in ♂.

Biology: Females suck haemolymph from adult insects of many orders; *F. collinsi* and *monoplectron* have been taken on butterflies, and *insignicornis* on mosquitoes and small crane flies. Larvae feed on moss on rotting logs or on decaying wood with algae and moss (Saunders, 1964).

Distribution: Worldwide; 41 species.

Afrotropical species:
caliginosa Ingram & Macfie, 1924*a*: 386 (*Lasiohelea*). Ghana.
collinsi Lane, 1977: 308. Ethiopia.
consortis de Meillon & Wirth, 1989*b*: 212. South Africa.
geometrica Clastrier, 1959*b*: 437 (*Lasiohelea*). Réunion.
insignicornis Macfie, 1947: 29 (*Lasiohelea*). Uganda.
monoplectron Lane, 1977: 306. Tanzania; Nigeria.

Subgenus *Warmkea* Saunders

(Figs 83, 129, 131, 133)

Forcipomyia, subgenus *Warmkea* Saunders, 1956: 671. Type species, *Forcipomyia bicolor* Saunders, by original designation.

Reference: Saunders, 1956: 671 (revision, all stages).

Diagnosis: Pale yellowish, slender midges, more slender and less setose than most *Forcipomyia*. Antenna exceptionally elongate, with marked increase in lengths between segments 10 and 11 in ♀. Palpus 4-segmented, segments four and five completely fused; third segment with sensilla not borne in definite pit. ♀ with mandibular teeth. Mesonotum often with conspicuous median infuscated vitta. Wing unmarked, with moderately dense macrotrichia; costal ratio 0,49–0,62; second radial cell closed or nearly so, narrow, twice the usual length in *Forcipomyia s. s.* Legs moderately bristly, tibiae without hastate spines; claws of ♀ (Fig. 129) broad at middle; empodium well developed in both sexes; tarsal ratio 1,30–2,10. ♀ with one spermatheca, neck often long and oblique. ♂ genitalia with same general structure as in subgenus *Forcipomyia*, dististyles often curved, hooklike.

Immature stages (after Saunders 1956): Larva (Fig. 131) colourless, with pale or dark head; prognathous; body setae considerably reduced in number and size, some bifid or multiple; *a* setae minute, spear-shaped; prothoracic pseudopod abruptly conical; cauda short, bluntly conical or more tapering, finely setulose. Pupa (Fig. 133) with various knobby and spiny processes on thorax and abdomen; prothoracic respiratory horn broad at base, projecting to angular knob on posterior surface, neck narrow, head rounded, bearing numerous spiracular openings in row over top; larvae exuviae not retained; ♂ genital processes dorsal.

Biology: Adults are attracted to flowers. Larvae are found in leaf axils of *Pandanus*, aroids, and epiphytic and terrestrial bromeliads, and less often in rotting cacao leaves on the ground, in banana stems, and in bracts of *Heliconia* (Saunders, 1956).

Distribution: Pantropical; 13 species.

Afrotropical species:
brunnea de Meillon & Downes, 1986: 151. South Africa.
kaufmannae Wirth & Derron, 1976: 230. São Tomé).

SUBFAMILY DASYHELEINAE

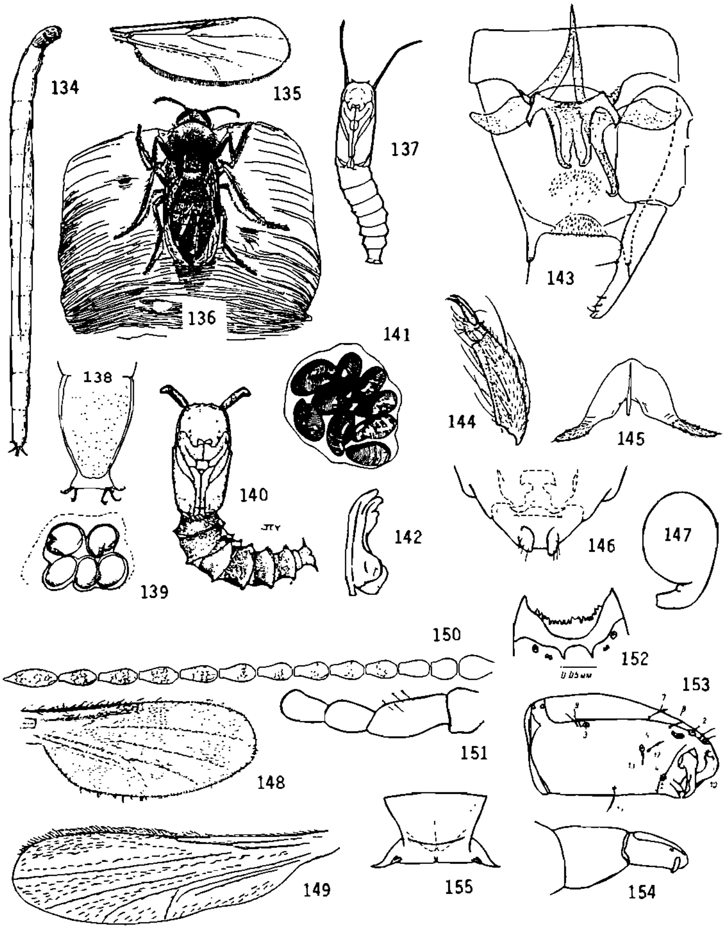
Only one genus, *Dasyhelea* Kieffer, which characterises the subfamily.

Genus *Dasyhelea* Kieffer

(Figs 134–155)

Dasyhelea Kieffer, 1911c: 5. Type species, *Dasyhelea halophila* Kieffer, by original designation.

Reference: Carter *et al.*, 1921: 178 (morphology, immature stages; Afrotropical species; de Meillon, 1942*a*: 11 (key to *fusca* species group); de Meillon & Downes, 1986: 155 (key to *salta* species group).



Figs 134–155. *Dasyhelea* spp.: 134, 140–142, *D. hawaiiensis* Macfie; 135–139, *D. calvescens* Macfie; 143, 149, *D. matubae* de Meillon; 144, *D. pseudoincisurata* Waugh & Wirth; 145–148, 150–151, 155, *D. hitchcocki* Wirth; 152–153, *D. modesta* (Winnertz); 134, larva; 135, 148, female wing; 136, female habitus; 137, 140, pupa; 138, larva, last segment; 139, 141, eggs; 142, larval mandible; 143, male genitalia; 144, female head, frontal sclerite; 145, female, precoxal bridge; 146, female genitalia; 147, female spermatheca; 149, male wing; 150, female antenna; 151, female palpus; 152, larval pharyngeal sclerites; 153, larval head; 154, larva, head and prothorax; 155, pupa, last abdominal segment.

Note: Several subgenera have been proposed and used for the Nearctic and Palaearctic *Dasyhelea*, but their use has been limited because of the inadequately described older species, and they have not been applied to the Afrotropical species.

Diagnosis: Body (Fig. 136) short, stout, and moderately setaceous. Eyes pubescent, contiguous. Antennal flagellar segments of ♂ (Fig. 150) with characteristic sculpturing to some degree; in ♀ with last five segments not greatly elongated. Palpus (Fig. 151) slender, reduced to four apparent segments, third (antepenultimate) segment with sensilla not borne in a sensory pit. Mandible nonfunctional, without sclerotised teeth. Mesonotum without humeral pits, usually without long setae. Wing (Fig. 148) usually unmarked, broad; with fine microtrichia; macrotrichia present, often arranged with bare lines along veins, sometimes setiform; costa usually reaching to about middle of wing; first radial cell obliterated, second small or obliterated. Prothorax with a variably developed precoxal bridge (Fig. 145). Legs slender, unarmed; hind basitarsus usually at least twice as long as second tarsomere; claws small and equal in both sexes; empodium small, not visible below 400x (Fig. 144). ♀ abdomen short and broad, with a sclerotised subgenital plate above sterna 8 and 9 (Fig. 146); 1–3 spermathecae (Fig. 147). ♂ abdomen slender; genitalia (Fig. 143) usually with rather long apicolateral processes on ninth tergum; ninth sternum often more or less fused with base of aedeagus; aedeagus broad, usually with paired caudal processes; parameres usually asymmetrical, with paired basal apodemes and single posterior process.

Immature stages: Larva (Fig. 134) moderately slender, body somewhat curved, without prominent setae or processes. Head capsule (Figs 153–154) well sclerotised, obovate, more or less hypognathous; eyes reniform, situated well forward. Mandible (Fig. 142) 3-toothed; pharyngeal skeleton with six combs, pharyngeal angulus with well-developed teeth (Fig. 152). Anterior pseudopod absent; posterior end of body with retractable pseudopod, making last segment appear double when extended; pseudopod bearing 10–12 anteriorly directed hooks and some fine spinules (Fig. 138); retractile filamentous anal papillae present. Pupa (Figs 137, 140) free from larval exuviae, rather stout, but conical in shape as the rule in the family; prothoracic respiratory horn elongate, of various shapes, usually diagnostic for the species; anal segment (Fig. 155) bearing, besides the usual caudal processes, two pairs of small protuberances ending in caudally directed setae. Egg (Figs 139, 141) with characteristic C-shape with ends doubled back against each other; deposited in a glutinous mass containing 15–20 eggs.

Biology: Females are not known to suck blood, meals apparently confined to nectar and plant juices; adults frequently abundant on flowers. Larval habits most often associated with algae, either algal growth on damp soil, mud, or sand, blanket algae on ponds or puddles; often in shallow accumulations of water in rocks, rain gutters, tree holes, plant leaf axils and other phytotelmata; in slightly moist decaying plant materials; often in extremely saline habitats; some species resistant to desiccation when habitat dries out. Adults of some tropical species are important pollinators of crops such as cocoa. Larval habitat records have been recorded for 18 Afrotropical species.

Distribution: Worldwide; 404 species.

Afrotropical species: The Afrotropical Catalogue lists 80 species; additions and corrections:

atra de Meillon & Wirth, 1989*b*: 213. Zimbabwe.
cellulana de Meillon & Wirth, 1983*a*: 353. South Africa.
columna de Meillon & Wirth, 1989*b*: 213. Zimbabwe.
davidi Clastrier, 1983*c*: 27. Seychelles.
falcata de Meillon & Downes, 1986: 152. South Africa.
fontana de Meillon & Wirth, 1981*b*: 533. South Africa.
forficata de Meillon & Wirth, 1989*b*: 215. Senegal.

fosteri Clastrier, 1983*c*: 28. Seychelles.
fulvithorax Kieffer, 1911*b*: 338 (*Culicoides seychelleanus* var.). Seychelles.
hamata de Meillon & Wirth, 1989*b*: 217. Zimbabwe.
imperfecta de Meillon & Wirth, 1989*b*: 217. Zimbabwe.
latiforceps Clastrier, 1983*c*: 29. Seychelles.
leporis de Meillon & Wirth, 1981*b*: 572. South Africa.
monosticta Ingram & Macfie, 1923: 60 (*Thysanognathus*). Zanzibar; Aldabra.
salinaria de Meillon & Wirth, 1981*b*: 530. South Africa.
salta de Meillon & Downes, 1986: 155. South Africa.
soutini de Meillon & Wirth, 1987*a*: 38. South Africa.
speciosa Clastrier, 1983*c*: 34. Seychelles.
upsilon de Meillon & Wirth, 1987*a*: 39. South Africa.

SUBFAMILY CERATOPOGONINAE

Diagnosis: Size ranging from smallest to largest in the entire family; wing length 0,4–5,0 mm. Body and legs slender to stout (Figs 1, 160, 288, 374); fifth tarsomeres with empodium small to absent. Wing with costa short to long; one or two radial cells, rarely both obsolete; crossvein r–m present; intercalary vein in cell R5 not prominent. Antenna 15-segmented; distal five segments usually elongate in ♀, distal 3–4 elongated in ♂; last segment without terminal papilla, often with terminal seta. Palpus typically 5-segmented, segment 3 with sensory pit usually small. ♀ ninth sternum divided medially; cerci short; ♂ genitalia variable.

Immature stages: Larva with distinctive, elongate, eel-like form and prognathous, more or less elongated head. Body setae minute except on last segment; cuticle smooth, whitish or translucent; no prolegs (except in first instar of some *Culicoides*).

Biology: Larval habitats range from semi-aquatic, burrowing in moist soil or sphagnum mats, to fully aquatic and free swimming; some genera in benthos and plankton of large lakes and streams. Feeding habits usually carnivorous. Adult feeding habits vary according to tribe (Downes 1978).

Classification: Six tribes are included in the subfamily Ceratopogoninae: Culicoidini, Ceratopogonini, Heteromyiini, Sphaeromiini, Palpomyiini, and Stenoxenini, all of which occur in the Afrotropical Region. Following Wirth & Grogan (1988) the tribe Stilobezziini of earlier workers is combined with the Ceratopogonini.

Tribe Culicoidini

Taxonomic notes: The tribe Culicoidini comprises two genera, *Culicoides* Latreille and *Paradasyhelea* Macfie. Wirth & Lee (1958) assigned the Australian bloodsucking genus *Austroconops* Wirth & Lee to the Culicoidini but recently Borkent *et al.* (1987) studied the male of *Austroconops mcmillani* Wirth & Lee and found it to be distantly related and they removed the species to a separate subfamily, the Austroconopinae. Boorman & Lane (1979) described a new genus and species, *Neoculicoides taylori*, from Nigeria which they placed in the tribe Culicoidini, but after examining paratypes of this species we are of the opinion that it is actually an atypical member of the *Culicoides* subgenus *Diphaomyia* Vargas. In any case the name *Neoculicoides* Boorman & Lane is a junior homonym of *Neoculicoides* Pierce (1966), described from a silicified fossil pupa from the Miocene of California. *Paradasyhelea* is known only from four species from temperate Australia and New Zealand, one species from Patagonia, and one species from western North America. The immature stages of *Paradasyhelea* are almost identical with those of *Culicoides* but the adults differ in many features, such as wing vestiture, oblique r–m crossvein, presence of scattered sensilla basiconica on the antenna, 3–4 segmented palpus, and in structure of the male genitalia. Since *Culicoides* is the only genus of Culicoidini in our area, the diagnosis of the genus will serve to diagnose the tribe.

Genus *Culicoides* Latreille

Culicoides Latreille, 1809: 251. Type species, *Culicoides punctatus* Latreille, by monotypy.

References: Carter, Ingram & Macfie, 1920: 211 (morphology; descriptions of West African species); Colaco, 1946: 235 (key to Afrotropical species); Fiedler, 1951: 3 (key, synopsis, figs.; South African species); Caeiro, 1961: 1 (revision Angolan species); Cornet, 1969: 341 (West African species); Nevill, 1969: 165 (morphology, key, immature stages; South African species); Cornet & Chateau, 1970 (revision of *similis* Group); Khamala & Kettle, 1971: 1 (revision East African species); Lubega & Khamala, 1976: 421 (larvae habitats; Kenya); Boorman & Dipeolu, 1979: 1 (revision Nigerian species); Cornet & Nevill, 1980 (plain-wing species); Glick, 1990: 85 (revision, Kenya).

Remarks: *Culicoides* is a large and important genus, with nearly 1 200 described species worldwide, and nearly 150 named Afrotropical species. Their great economic importance as economic pests because of their bloodsucking habits and transmission of pathogens of man and domestic animals has resulted in a significant amount of research in the Afrotropical Region on their taxonomy and biology, as indicated in the references above. A review of this work, and a synopsis of the Afrotropical species is beyond the scope of this publication, and needs to be dealt with elsewhere. Fortunately such studies are now in progress at the Onderstepoort Veterinary Research Laboratory by Rudy Meiswinkel, and hopefully will result in a comprehensive revision of the genus.

Although some 24 subgenera of *Culicoides* have been proposed and used in various parts of the world, workers in Africa have not made use of them. The three most recent and comprehensive works (Khamala & Kettle 1971, Boorman & Dipeolu 1979, Glick 1990) for good reason used species groups for their classification. The adoption of subgenera and the correct assignment of species have nomenclatural implications that require in-depth revisionary studies of region-wide, if not world-wide faunas.

Diagnosis: Small to medium size midges (Fig. 1); wing length 0,8–2,0 mm. Body moderately setaceous, strong setae or spines absent. Mesonotum with well-developed humeral pits. Head and mouthparts as in Fig. 3; antenna with sensilla coeloconica always present on segment 3, and varying according to taxonomic group also in a definite pattern on distal flagellar segments; pattern of sensilla trichodea distribution also useful taxonomically. Palpus 5-segmented, third segment variably swollen and bearing a characteristic sensory pit or sensory area. Proboscis well developed, the mandibles with numerous fine teeth for feeding on vertebrates (rarely reduced or absent). Legs slender, without spines; basitarsi without ventral palisade setae (bulbous setae); fourth tarsomeres cylindrical (rare exceptions); ♀ claws short, equal, and simple on all legs; empodium present but small. Wing (Fig. 1) with distinct microtrichia and usually with abundant macrotrichia; usually with a distinct colour pattern of round or irregular pale areas on a dark background. Costa usually short, costal ratio 0,5–0,7; two radial cells usually present, rarely obsolescent; media petiolate, base of vein M2 usually obsolescent (Fig. 2). ♀ abdomen moderately stout; sclerotised spermathecae from none to three. ♂ genitalia (Fig. 4) variable in structure according to subgenus or species group; ninth tergum usually long and tapered, with well-developed apicolateral processes, ninth sternum short with shallow caudomedian excavation; aedeagus and parameres variable.

Immature stages (Figs 5–24): Larva slender and vermiform, 2–5 mm long when mature. Head capsule (Figs 5–7) yellowish to brownish and body translucent whitish, usually with some patches of subcutaneous pigment in characteristic pattern on thoracic segments. Setae of head and body short and inconspicuous, except sometimes for a group of perianal setae. Head capsule (Fig. 6) separated by a moulting suture into two sclerites, the dorsomedian frontoclypeus, and the remainder of the head capsule. Letter designations of the head setae (Figs 5–7) follow Saunders (1924), Lawson (1951), Kettle & Lawson (1952), and Blanton & Wirth (1978). A simple or pigmented eyespot located on each side of head at about midlength. Mouthparts (Fig. 10) arranged as in the diagram by Lawson (1951); pharyngeal apparatus (Fig. 8) consisting of a ventral hypopharynx and a dorsomedian epipharynx, the latter composed of a series of usually four overlapping combs, whose shape and arrangement are useful in larval classification. *Culicoides* pupae (Figs 13–14) range from 2 to 5 mm in length, of typical ceratopogonid shape, stout anteriorly and tapering caudad; prothoracic respiratory horn (Fig. 22) usually elongated and bearing a characteristic series of lateral and terminal spiracular openings. Tubercles and setae of cephalothorax (Fig. 15) and abdomen (Figs 16, 21) arranged in characteristic pattern, varying somewhat from group to group; the system of chaetotaxy devised by Carter *et al.* (1920) has been followed rather uniformly by current workers. Setation and armature of operculum (Fig. 18), the sclerite lying between the arms of the molting suture on the cephalothorax, is also useful. Last abdominal segment (Fig. 24) ending in a pair of laterally directed spine-like processes.

Biology: Reviews of published information on biology and control of *Culicoides* worldwide were presented by Kettle (1962, 1969, 1977). In South Africa Nevill (1969) described methods of collecting, rearing, and studying all stages, by which he was able to obtain and describe the larvae of eight species and pupae of seven species. In Zimbabwe Braverman (1978) reared 19 species from their larval habitats, which he described and classified. The most important larval habitats were mud around water bodies, especially dams, puddles rich in organic matter, drainage canals, cattle dung, and rot holes in tree forks. Meiswinkel (1987, 1989) and Dyce & Marshall (1989) reported on the breeding habits of one group of species in dung of cattle and wild game animals in South Africa. Nevill *et al.* (1988) reported on the blood-feeding habits of species associated with livestock in the western Cape Province, and their larval habitats in irrigated pastures.

Tribe Ceratopogonini

Reference: Wirth & Grogan, 1988: 1 (world revision; keys; diagnoses; figures).

Diagnosis: Slender to stout, usually predaceous midges (Fig. 160), minute to moderately large in size (wing length 0,4–2,5 mm). Eyes (Fig. 249) usually widely separated, bare or pubescent. Antenna variable in length; sometimes number of segments reduced; sensilla coeloconica often present on segment 3 (Figs 178, 191), and or sometimes on distal segments. Palpus variable, usually 5-segmented; third segment usually with small round sensory pit. ♀ mandible (Fig. 214) usually with 6–10 strong teeth adapted for feeding on insects. Thorax usually robust, humeral pits present or absent. Wing often with prominent colour pattern due to enlarged, pigmented microtrichia (Figs 160–161); macrotrichia present but sparse, or absent; usually two radial cells, one or both may be obliterated; costa usually to 0,6–0,7 of wing length; media petiolate (Figs 156, 159), vein M2 may be interrupted at base or absent. Legs variable, sometimes spiny, often one or more pairs swollen, sometimes conspicuously; femora armed ventrally with stout ventral spines, or unarmed; hind basitarsus with ventral palisade setae (Figs 230, 265); proximal tarsomeres often with some stout ventral spines (Figs 232–233); fourth tarsomeres cylindrical, subcylindrical, or if cordiform, usually provided ventrally at tip with a pair of hyaline sensory setae (Figs 195, 230); fifth tarsomeres rarely with strong ventral spines or batonnets; ♂ claws usually small and equal; ♀ claws usually enlarged, often unequally developed (Fig. 169) or dissimilar on one or more pairs of legs (Fig. 194), in some genera reduced to one long talon with or without a basal tooth (Fig. 289). ♀ abdomen usually short and stout (Fig. 160); one to three sclerotised spermathecae present. ♂ genitalia variable, usually short and stout; aedeagus usually with low basal arch and small distal process (Figs 162, 190); parameres usually separate with slender basal apodemes (Figs 163, 183), modifications characteristic for each genus.

Immature stages: Larva vermiform, without prolegs; head capsule well sclerotised, with mouthparts arranged for predaceous feeding habits; head and body setae usually inconspicuous, not enlarged in anal area. Pupa (Figs 165–166) of usual ceratopogonid conformation with large cephalothorax and straight tapering abdomen; proportions variable from slender to stout; prothoracic respiratory horn (Figs 164, 286) short to long, shape and arrangement of spiracular openings diagnostic for the genus; thorax often with conspicuous dorsal tubercles; abdomen sometimes with segmental spines well developed.

Biology: Females are predaceous on small soft-bodied insects such as Chironomidae. Larval habits are various, some sluggish and crawling through damp moss or algae in semi-aquatic habitats, some swimming vigorously at water surface or in deeper waters; others creeping through algal mats or wet soil.

Genus *Afrohelea* Wirth

(Figs 156–158)

Afrohelea Wirth, 1965: 230. Type species, *Parabezzia capensis* de Meillon & Hardy, by original designation.

Diagnosis: Small, shiny, dark brown midges. Eyes narrowly separated, with minute interfacetal setae. Antenna with distal five flagellar segments elongated in both ♂ and ♀; ♂ antenna without plume. Palpus 5-segmented, third segment with prominent sensory pit. Legs moderately robust, with numerous stiff setae; femora unarmed ventrally; tarsi with ventral spines at base and apex of first two tarsomeres on mid and hind legs; fourth tarsomeres deeply cordiform; fifth tarsomeres elongated and slender, unarmed; ♀ claws large, equal, each talon with inner basal tooth (Fig. 157). Wing (Fig. 156) without colour pattern; one long radial cell; costal ratio 0,6–0,8; costa not produced beyond end of R4 + 5. ♀ with two spermathecae. ♂ genitalia (Fig. 158) with ninth tergum narrow distally with distolateral wing-like plates; basistyle large and bulbous, dististyle slender; aedeagus bell-shaped in ventral profile, with slender tip; parameres separate, each with short basilateral process and slender, subapically truncate, distal process with slender extensions.

Immature stages and Biology: Unknown.

Distribution: South Africa; l species.

Included species:

capensis de Meillon & Hardy, 1954: 67 (*Parabezzia*). South Africa.

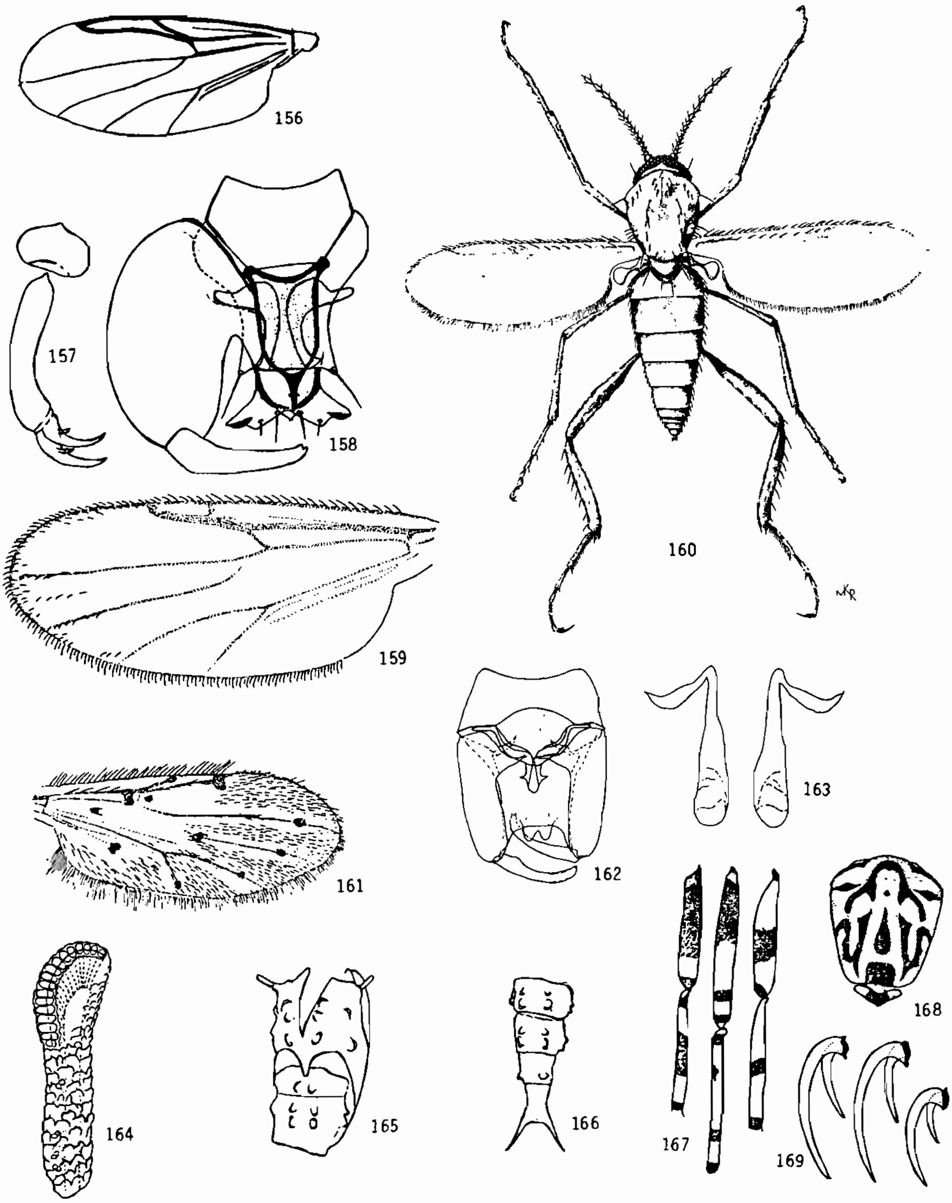
Genus *Allohelea* Kieffer

(Figs 160, 165–166, 177)

Allohelea Kieffer, 1917*b*: 364. Type species, *Sphaeromias pulchripennis* Kieffer, by original designation.

Diagnosis: Moderately large, stout midges (Fig. 160); wing length 1,2–2,0 mm. ♀ antenna moderately long; ♂ antenna with plume, flagellar segments separate. Palpus 5-segmented; third segment moderately swollen, with small round sensory pit. Wing (Fig. 160) with three large dark anterior spots and irregular posterior infuscated areas usually of same intensity; venation as in *Monohelea*; media sometimes with bead-like swelling near base; costal ratio 0,72–0,84. Hind leg swollen and shining black, with pale knee spot. Hind tarsus short and bearing strong ventral spines at apices of proximal 2–4 tarsomeres; 4th tarsomeres of fore and mid legs cylindrical, of hind leg elongate; claws of fore and mid legs of ♀ short, bent basally, straight distally, with basal inner and outer teeth and bifid tips; in ♂ small, equal and simple; hind claw of ♂ and ♀ single, long, with short basal tooth. Two equal spermathecae. ♂ aedeagus without basal loop, the slender, pointed distal process borne in a notch in the quadrate basal sclerite; parameres of various shapes (Fig. 177).

Immature stages: Larva undescribed. Pupa (of *M. mimas* de Meillon, 1939*a*) (Figs 165–166) stout and tapering, cephalothorax and abdomen with well-developed dorsal tubercles, these covered with small nodules, but without setae



Figs 156–169. Tribe Ceratopogonini: 156–158, *Afrohelea capensis* (de Meillon & Hardy); 159, *Ankylohelea montana* de Meillon & Wirth; 160, *Allohelea nebulosa* (Coquillett); 161–163, *Alluaudomyia bella* (Coquillett); 164, *Alluaudomyia needhami* Thomsen; 165–166, *Allohelea mimas* (de Meillon); 167–169, *Alluaudomyia inexspectata* Clastrier; 156, 159, 161, female wing; 157, female hind tarsomeres 4 and 5; 158, 162, male genitalia; 160, female habitus; 163, male parameres; 164, pupal respiratory horn; 165–166, pupa; 167, femora and tibiae, female; 168, dorsal thoracic pigmentation; 169, female claws.

or setae. Respiratory horn short and slender, with sides subparallel, mounted on a prominent pedestal, and bearing one lateral and five apical spiracular openings. Last segment bearing a pair of long, pointed, slightly diverging, apicolateral processes with sharp tips.

Biology: *Allohelea mimas* was reared from a pupa collected in a stream amongst grass.

Distribution: Worldwide, mainly Oriental; 34 species.

Afrotropical species:
africana Clastrier, 1960*a*: 282 (*Monohelea*). Rep. Congo.
litoraurea Ingram & Macfie, 1921: 344 (*Monohelea*). Ghana.
makonde de Meillon & Wirth, 1983*a*: 363 (*Monohelea*). South Africa.
maureenae de Meillon & Wirth, 1987*a*: 53 (*Monohelea*). South Africa.
meeseri de Meillon, 1959*b*: 16 (*Monohelea*). South Africa.
mimas de Meillon, 1939*a*: 13 (*Monohelea*). South Africa.
pulchripennis Kieffer, 1911*b*: 344 (*Sphaeromias*). Seychelles.
sylvatica Clastrier, 1960*a*: 284 (*Monohelea*). Rep. Congo.

Genus *Alluaudomyia* Kieffer

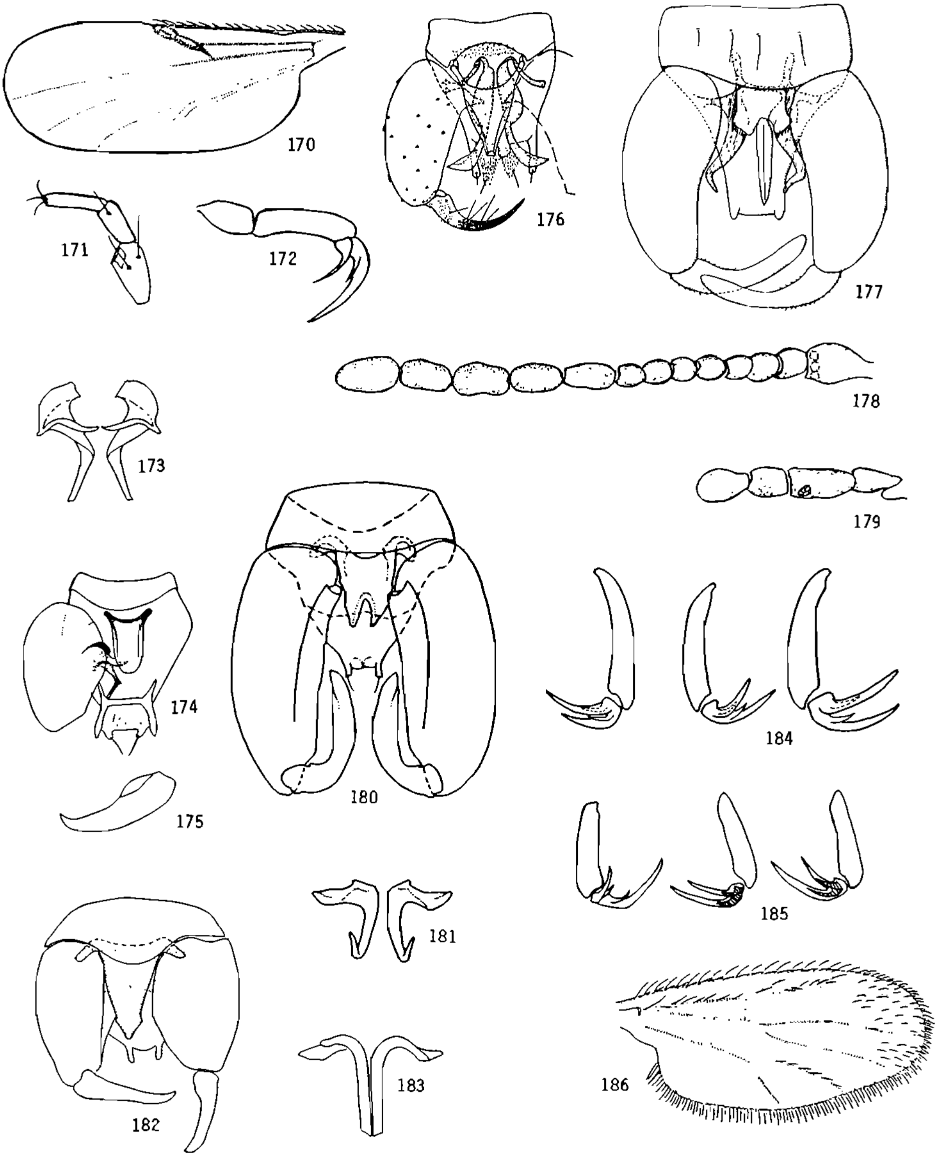
(Figs 161–164, 167–169, 176)

Alluaudomyia Kieffer, 1913*b*: 12. Type species, *Alluaudomyia imparunguis* Kieffer, monobasic.

Diagnosis: Small to medium sized setaceous midges; wing length 1–2 mm. Wing (Fig. 161), mesonotum (Fig. 168), and legs (Fig. 167) usually conspicuously ornamented. Eyes bare (rarely pubescent), contiguous or narrowly separated. Antenna of ♀ moderately slender, segments 11–15 elongated; ♂ antenna with plume, segments 4–12 more or less fused. Palpus 5-segmented, third segment slender with small sensory pit. Wing (Fig. 161) with one, rarely two, radial cells; first usually obliterated, second more or less well developed; wing without microtrichia, macrotrichia numerous on distal part of wing; usually 1–20 small dark spots present, and sometimes greyish streaks along veins. Legs (Fig. 167) slender, more or less setaceous; fourth tarsomeres cordiform; ♀ claws (Fig. 169) long, usually very unequal, sometimes subequal on fore and mid legs, very unequal on hind leg, without basal inner tooth. ♀ with one or two spermathecae. ♂ genitalia (Figs 162, 176) with ninth tergum usually long and usually with well-developed apicolateral processes; aedeagus arched with large distal process; parameres (Fig. 163) divided, shape varies with species, slender basistylar apodeme present.

Immature stages: Larva with head about twice as long as broad, slightly tapering anteriorly, setae well-developed, slender; last segment about three times longer than broad, perianal setae strong, as long as last segment. Pupa with respiratory horn (Fig. 164) short to moderately long, often expanded distally with spiracular openings borne in a broad double palisade around distal portion.

Biology: Larvae are predaceous, aquatic; swimming actively at the water surface, or at the surface film at the water line on algae, wet wood, or emergent vegetation. Mayer (1955) described and figured the immature stages of *A. maculithorax*



Figs 170–186. Tribe Ceratopogonini: 170–175, *Brachypogon (Isohelea) africanus* (de Meillon); 176, *Alluaudomyia inexspectata*; 177, *Allohelea johannseni* Wirth; 178–179, *Brachypogon (Isohelea) stigmalis* (Coquillett); 180–181, 184, *Ankylohelea montana*; 182–183, 186, *Calcarhelea bimater* (de Meillon & Hardy); 185, *Bothahelea phelpsi* Grogan & Wirth; 170, 186, female wing; 171, female palpal segments 3–5; 172, female hind leg, tarsomeres 4–5; 173, 181, 183, male parameres; 174, male genitalia (partial); 175, male dististyle; 176–177, 180, 182, male genitalia; 178, female antenna; 179, female palpus; 184–185, female fifth tarsomeres.

(Carter, Ingram & Macfie) and the pupa of *A. claudia* de Meillon and *A. natalensis* de Meillon. Wanson (1939) reared *A. albopictus* (Ingram & Macfie), *A. maculipennis* (I. & M.), and *A. melanostictus* (I. & M.) from quiet water with organic debris on stream margins with abundant vegetation in Zaïre. The larvae were predatory on larvae of *Forcipomyia*, but in turn were preyed on by *Hydrobius* (Coleoptera) larvae. There are six other published Afrotropical records of habitats of *Alluaudomyia* larvae from a pond, a stream, from stagnant water containing much organic matter, from water with *Spirogyra* algae, from swampy mud, and from a rot hole in a mango tree.

Distribution: Worldwide; 170 species.

Afrotropical species: The Afrotropical Catalogue lists 36 species; additions and corrections:
cobra de Meillon & Wirth, 1987*a*: 41. South Africa.
imperfectus Goetghebuer, 1935: 172 (*Culicoides*). Zaïre. To *Fanthamia*.
inexspectata Clastrier, 1983*c*: 10. Seychelles.
libanius de Meillon, 1943: 104 (*Ceratopogon*). South Africa.
louisi de Meillon & Wirth, 1981*b*: 535. South Africa.
magoebai de Meillon, Meiswinkel & Wirth, 1982: 134. South Africa.
meeseri de Meillon & Hardy, 1954: 74 (*Ceratopogon*). Zimbabwe.
rudolfi de Meillon & Downes, 1986: 171. South Africa.
spinosiforceps Clastrier, 1977: 345. Rep. Guinea.

Genus *Ankylohelea* de Meillon & Wirth

(Figs 159, 180–181, 184)

Ankylohelea de Meillon & Wirth, 1987*b*: 384. Type species, *Ankylohelea montana* de Meillon & Wirth, by original designation.

Diagnosis: Small brown midges, wing length 1,0 mm. Eyes narrowly separated, setaceous. Antenna moderately long; distal five segments of ♂ and ♀ slightly elongated; ♂ flagellar segments not fused, plume reduced to sparse long verticils. Palpus 5-segmented, third segment with shallow round sensory pit. Legs moderately slender, hind femur slightly enlarged; femora unarmed; fourth tarsomeres cordiform, fifth unarmed; ♂ and ♀ claws (Fig. 184) subequal and similar on all legs, moderately strong and curved, each talon with basal inner tooth. Wing (Fig. 159) without colour pattern; costal ratio 0,62–0,69; two radial cells, first slit-like, second twice as long as first and moderately broad; base of media narrowly interrupted. ♀ abdomen with segments 7 and 8 narrowed and strongly sclerotised, 8 forming a complete ring; two oval spermathecae. ♂ ninth tergum short and tapering, apicolateral processes moderately short and close together; basistyle elongate, dististyle abruptly bent or elbowed near base (Fig. 180). Aedeagus short and broad, basal arms short and stout, distal portion with deep apical incision. Parameres (Fig. 181) separate; basistylar apodeme strong; distal portions nearly straight, slender, with distal points directed ventrad over shoulders of aedeagus.

Immature stages and Biology: Unknown.

Distribution: South Africa; 1 species.

Included species:
montana de Meillon & Wirth, 1987*b*: 384. South Africa.

Genus *Bothahelea* Grogan & Wirth

(Fig. 185)

Bothahelea Grogan & Wirth, 1983: 159. Type species, *Bothahelea phelpsi* Grogan & Wirth, by original designation.

Diagnosis: Small midges, wing length 0,9–1,0 mm. Eyes broadly separated, minutely pubescent. Antenna with third segment bearing sensilla basiconica; ♂ flagellar segments not fused. Palpus 5-segmented, third segment with well-defined sensory pit. Fourth tarsomeres cylindrical, bearing apical whip-like hyaline sensilla; ♀ claws (Figs 185) long, subequal, each with long basal inner tooth. Wing with two radial cells, second twice as long as first; costal ratio 0,65–0,70. ♀ eighth segment a complete sclerotised ring; one large spermatheca and a small vestigial one. ♂ genitalia large and bulbous; ninth tergum narrow and elongate with wing-like distolateral expansions; aedeagus with three or more apical projections; parameres separate.

Immature stages and Biology: Unknown.

Distribution: Southern Africa; 3 species.

Included species:
gigantostyla Grogan & Wirth, 1983: 203. Zimbabwe.
nama de Meillon & Wirth, 1987*a*: 42. South Africa.
phelpsi Grogan & Wirth, 1983: 200. Zimbabwe.

Genus *Bothamia* Meiswinkel

Bothamia Meiswinkel, 1987: 300. Type species, *Bothamia demeilloni* Meiswinkel, by original designation.

Diagnosis: Small yellowish brown midges; wing length 0,78 mm. Eyes narrowly separated; strongly pubescent. ♀ antenna with sensilla coeloconica on segments 12–14; ♂ antenna with plume, segments 4–12 fused, sensilla coeloconica on segment 14. Palpus stubby, 5-segmented; palpal ratio 1,2. Legs slender, femora unarmed; fourth tarsomeres cordiform; fifth unarmed, slender; ♀ claws unequal on all legs. Wing with dense macrotrichia, without ornamentation; two small radial cells; vein M2 interrupted at base; costa short, costal ratio 0,50. ♀ abdomen pearly white, stout; two ovoid spermathecae and vestigial third. ♂ genitalia small, without apicolateral processes on ninth tergum; aedeagus with high basal arch and two distomedian projections; parameres a pair of broad arcuate blades, narrowly joined near midportion, distal portions flaring ventrolaterally.

Immature stages and Biology: Unknown.

Distribution: South Africa; 1 species.

Included species:
demeilloni Meiswinkel, 1987: 300. South Africa.

Genus *Brachypogon* Kieffer
(Figs 170–175, 178–179)

Synonymy under subgenera.

Diagnosis: Small to minute blackish midges; wing length 0,5–1,0 mm. Eyes pubescent, contiguous. Antenna with 15 segments, rarely 14 in ♀, as few as 11 in ♂; segments 4–13 of ♂ usually fused; segment 3 with sensilla coeloconica (Fig. 178). Palpus (Figs 171, 179) 5-segmented. Legs rather stout; femora unarmed, not swollen; fourth tarsomeres cylindrical to cordiform, each with a pair of long recurved whip-like sensilla; fifth tarsomeres unarmed; ♀ claws small to moderately long, subequal to unequal, usually with basal inner teeth, and often also with outer basal teeth (Fig. 172). Wing (Fig. 170) with radial cells variable, often completely obsolete; radial veins thick; costal ratio less than 0,65; vein M2 variable, absent or present and obsolete on base only. ♀ eighth segment entire, not divided by pleura; one or two spermathecae. ♂ genitalia (Figs 174–175) without long apicolateral processes on ninth tergum; parameres separate or fused.

Immature stages: Larval head stout, scarcely tapering anteriorly, a strongly sclerotised ventral seam caudally; head setae *x* and *s* multiple; antenna prominent; dorsal comb of epipharynx with 9 teeth on each side and no median tooth, a flat, wing-like plate with serrated edge on each lateral arm; anal segment with a circlet of relatively stout long dark perianal setae. Pupa with dark nodules dorsally on thorax; respiratory horn short and stout, L/W ratio about 4,0, very dark, about 6 spiracular openings in a row at apex.

Biology: *Brachypogon africanus* was reared from a pupa collected in an unshaded pool.

Subgenus *Brachypogon* Kieffer

Brachypogon Kieffer, 1899: 69. Type species, *Ceratopogon vitiosus* Winnertz, by original designation.

Diagnosis: Antenna of ♀ with 15 (rarely 14) segments; of ♂ usually with 15, but often reduced to 11 to 14 segments, 4–13 usually fused. Fourth palpal segment with 0–1 setae (rarely 2). One, rarely 2 spermathecae. Wing with first or second radial cell, or usually both, not formed; vein M2 usually completely absent; wing membrane without macrotrichia.

Distribution: Worldwide; 26 species.

Afrotropical species:
bergensis de Meillon & Hardy, 1953: 26 (*Ceratopogon*). South Africa.
brazzai Vattier & Adam, 1966*b*: 736 (*Ceratopogon*). Rep. Congo.
corius de Meillon & Hardy, 1954: 69 (*Ceratopogon*). South Africa.
emphuxi Vattier & Adam, 1966*b*: 734 (*Ceratopogon*). Rep. Congo.
grobleri de Meillon & Wirth, 1981*c*: 575. South Africa.
hamiltoni de Meillon & Wirth, 1981*c*: 576. South Africa.
krugeri de Meillon & Wirth, 1981*c*: 578. South Africa.
libanius de Meillon, 1943: 104 (*Ceratopogon*). South Africa.
mireillae Vattier & Adam, 1966*b*: 733 (*Ceratopogon*). Rep. Congo.
senegalensis de Meillon & Wirth, 1955: 275 (*Ceratopogon*). Senegal.
sitius de Meillon, 1959*a*: 345 (*Ceratopogon*). South Africa.

Subgenus *Isohelea* Kieffer

(Figs 170–175, 178–179)

Isohelea Kieffer, 1917*b*: 295. Type species, *Ceratopogon lacteipennis* Zetterstedt, sensu Kieffer [misidentified = *Psilohelea sociabilis* Goetghebuer], by original designation.

Diagnosis: Similar to *Brachypogon*, but with two well-developed radial cells (Fig. 170) of about equal size; vein M2 usually present; wing membrane usually with macrotrichia near margin. Fourth palpal segment with two setae (rarely one). Usually two spermathecae.

Distribution: Worldwide; 51 species.

Included species:
aethiopicum Clastrier, Rioux & Descous, 1961: 87 (*Ceratopogon*). Chad.
africanus de Meillon, 1929: 248 (*Ceratopogon*). South Africa.
albipennis Kieffer, 1921*b*: 22 (*Nilohelea*). Sudan.
hamoni Vattier & Adam. 1966*b*: 730 (*Ceratopogon*). Rep. Congo.

Genus *Calcarhelea* Wirth & Grogan

(Figs 182–183, 186)

Calcarhelea Wirth & Grogan, 1988: 35. Type species, *Alluaudomyia bimater* de Meillon & Hardy, by original designation.

Diagnosis: Small brown midges with unmarked wing; wing length 1,3 mm. Eyes broadly separated; bare in ♀, pubescent in ♂. ♂ antenna without plume, last five flagellar segments elongated as in ♀. Palpus 5-segmented; third segment with indistinct sensory pit. Hind basitarsus with black ventral spine at base and at apex; fourth tarsomeres cordiform; ♀ claws subequal on fore and mid legs, unequal on hind leg, claws without basal inner tooth on fore and hind legs, with inner basal tooth on mid leg. Wing (Fig. 186) with two well-formed radial cells, posterior branch of radius strong, especially where it joins costa; costal ratio 0,72; macrotrichia dense in distal part of cell R5. Two spermathecae. ♂ genitalia (Fig. 182) with ninth tergum ending in a close-set pair of digitiform apicolateral processes; aedeagus with anterior margin transverse, basal arch not developed, tapering distally to bluntly pointed tip; parameres (Fig. 183) separate, basal apodemes slender and curved, distal portions nearly straight blades.

Immature stages and Biology: Unknown.

Distribution: South Africa; 1 species.

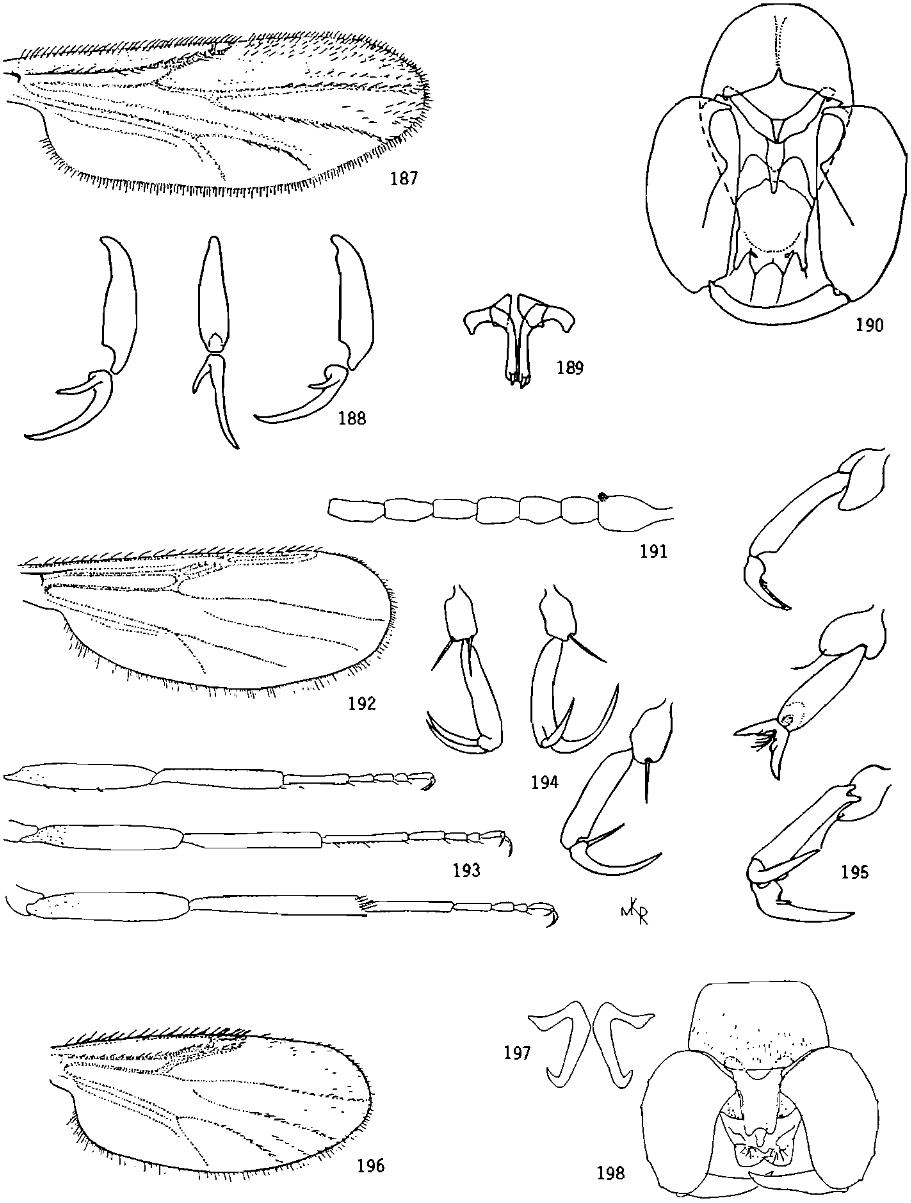
Included species:
bimater de Meillon & Hardy, 1953: 25 (*Alluaudomyia*). South Africa.

Genus *Capehelea* de Meillon & Wirth

(Figs 187–190)

Capehelea de Meillon & Wirth, 1987*b*: 387. Type species, *Capehelea steli* de Meillon & Wirth, by original designation.

Diagnosis: Medium size, uniformly brownish midges; wing length 1,40 mm. Eyes closely approximated, bare. Antenna moderately long, sensilla coeloconica present on segments 11–14 in ♀; ♂ antenna with dense plume, segments 4–12



Figs 187–198. Tribe Ceratopogonini: 187–190, *Capehelea steli* de Meillon & Wirth; 191–194, *Congohelea fuligipennis* (Clastrier); 195–198, *Ceratohelea advena* (de Meillon); 187, 192, 196, female wing; 188, 194–195, female tarsomeres 4–5; 189, 197, male parameres; 190, 198, male genitalia, parameres omitted; 191, female antennal segments 3–9; 193, female legs.

fused, 13–14 elongated. Palpus 5-segmented, third segment slightly expanded distally with small, deep sensory pit. Legs moderately slender, femora unarmed; fourth tarsomeres cordiform, bearing a pair of down-curved, hyaline sensilla; fifth tarsomeres unarmed; ♀ claws (Fig. 188) a single long talon with slender basal tooth half as long. Wing (Fig. 187) without pattern; a few macrotrichia on distal half; costal ratio 0,59; two radial cells, both complete and subequal in length, second broader; vein M2 interrupted a short distance at base. Two functional and one vestigial spermathecae, the former with a pedestal-like ring near the neck. ♂ genitalia (Fig. 190) with ninth sternum rather elongate with distinct median suture-like line; ninth tergum as long as basistyles, tapering to narrow apex with prominent apicolateral processes and a pair of submedian setose papillae. Aedeagus Y-shaped, about as wide at base as total length, basal arch to half of total length; distal process slender and lightly sclerotised. Parameres (Fig. 189) separate, basal arm winglike; distal process nearly straight, the pair closely approximated, slightly widening to rounded tip bearing a sharp, spurlike, ventromesal projection. Immature stages unknown.

Immature stages and Biology: Unknown.

Distribution: South Africa; 1 species.

Included species:
steli de Meillon & Wirth, 1987*b*: 388. South Africa.

Genus *Ceratohelea* Wirth & Grogan

(Figs 195–198)

Ceratohelea Wirth & Grogan, 1988: 40. Type species, *Ceratopogon advena* de Meillon, by original designation.

Diagnosis: Medium size blackish midges; wing length 1,6 mm. Eyes broadly separated, pubescent. Antenna with sensilla coeloconica on segment 14 in both sexes; ♂ antenna with proximal segments not fused, plume well developed. Palpus 5-segmented. Legs slender, femora unarmed; fourth tarsomeres markedly cordiform; ♀ claws (Fig. 195) small and subequal on fore and mid legs, moderately unequal on hind leg, each talon with small basal inner tooth. Wing (Fig. 196) with two subequal radial cells, first narrow, second broad and almost square-ended; costal ratio 0,63 in ♀; media with short petiole. Two small oval spermathecae and a vestigial third. ♂ genitalia (Fig. 198) short and broad; ninth sternum long, ninth tergum short, strongly tapered distally and ending in a pair of rounded, strongly sclerotised, flange-like lobes; basistyle stout, with strongly sclerotised dorsomesal lobe; aedeagus a trapezoidal-shaped structure, bearing a small tapering distomedian process; parameres (Fig. 197) separate, with long curving basal apodeme, main portion a slightly tapering, nearly straight rod, abruptly curved ventrad distally and ending in a blunt point.

Immature stages and Biology: Unknown.

Distribution: South Africa; 1 species.

Included species:
advena de Meillon, 1959*a*: 341 (*Ceratopogon*). Zimbabwe.

Genus *Congohelea* Wirth & Grogan

(Figs 191–194).

Congohelea Wirth & Grogan, 1988: 46. Type species, *Serromyia fuligipennis* Clastrier, by original designation.

Diagnosis: ♀ only. Small dark brown midge with brownish wing; wing length 0,98 mm. Eyes bare, with V-shaped separation. Antenna with sensilla coeloconica on third segment (Fig. 191). Palpus 5-segmented. Wing (Fig. 192) with two narrow radial cells, second twice as long as first; costal ratio 0,81; media with short petiole. Legs (Fig. 193) with pale bands; fore femur armed ventrally with three stout, widely spaced, short ventral spines in a series; fourth tarsomeres short and cylindrical on all legs, not cordiform, each with two sharp distolateral spines; claws (Fig. 194) subequal (4–3) on fore legs, unequal (5–2) on mid and hind legs, without basal inner teeth. One spermatheca.

Immature stages and Biology: Unknown.

Distribution: Rep. Congo; 1 species.

Included species:
fuligipennis Clastrier, 1960*a*: 291 (*Serromyia*). Rep. Congo.

Genus *Downeshelea* Wirth & Grogan

(Figs 199–201)

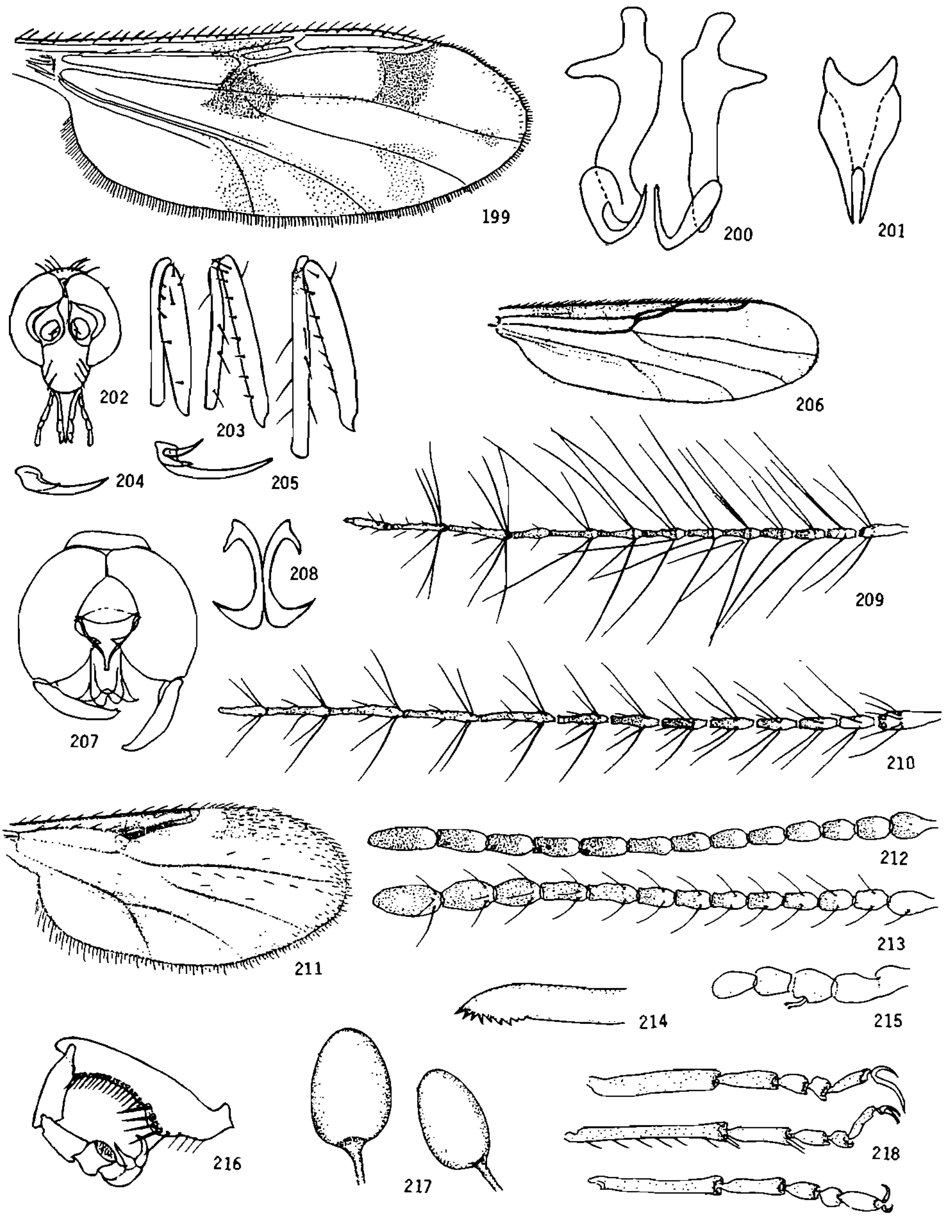
Downeshelea Wirth & Grogan, 1988: 50. Type species, *Monohelea stonei* Wirth, by original designation.

Diagnosis: Medium size, stout midges with ornamented wings; wing length 1,1–2,0 mm. Eyes contiguous, bare. Antenna with distal segments moderately elongated; ♂ with well-developed plume, segments not fused. Palpus 5-segmented. Legs slender, unarmed; femora and tibiae usually dark brown with yellowish knees; tarsomere 1 with sub-basal spine; tarsomere 4 of fore and mid legs cylindrical, of hind leg greatly elongated; ♀ claws rather long, curved, and equal-sized, with basal inner and outer teeth on fore and mid legs, hind claw single, elongated, without basal tooth; ♂ claws small and equal. Wing (Fig. 199) with two dark spots anteriorly, fainter markings along posterior veins; two radial cells, second twice as long as first, costal ratio 0,7 or more. ♀ abdomen with median sclerite between tips of sternum 9; two subequal spermathecae. ♂ genitalia with ninth sternum produced posteriorly, bearing a pair of large setae; ninth tergum with rather large, divergent, apicolateral processes; aedeagus (Fig. 201) a single piece without basal loop; parameres (Fig. 200) separate, of various shapes.

Immature stages and Biology: Unknown.

Distribution: Worldwide, mainly Neotropical; 23 species.

Afrotropical species:
nigeriae Ingram & Macfie, 1922: 268 (*Monohelea*). Nigeria.



Figs 199–218. Tribe Ceratopogonini: 199–201, *Downeshelea stonei* (Wirth); 202–205, *Echinohelea pastoriana* Clastrier; 206–210, *Echinohelea lanei* Wirth; 211–218, *Fanthamia cardinis* de Meillon & Wirth; 199, 206, 211, female wing; 200, 208, male parameres; 201, male aedeagus; 202, female head; 203, female femora & tibiae; 204, female fore leg, claws; 205, female mid leg, claws; 207, male genitalia, parameres omitted; 209, 213, male antenna; 210, 212, female antenna; 214, female mandible; 215, female palpus; 216, male hind tarsus; 217, female spermathecae; 218, female tarsi.

Genus *Echinohelea* Macfie

(Figs 202–210)

Echinohelea Macfie, 1940*b*: 187. Type species, *Echinohelea ornatipennis* Macfie, by original designation.

Diagnosis: Medium size yellowish to reddish brown midges; wing length 1,3–2,0 mm. Eyes bare, narrowly separated (Fig. 202). Antenna (Fig. 210) long and slender, verticils long; ♂ flagellum (Fig. 209) without plume, last five segments elongated as in ♀; third segment with numerous sensilla coeloconica. Palpus 5-segmented. Proboscis elongated. Legs rather stout (Fig. 203), spiny, especially in ♂ and with additional fine wavy setae; femora with strong, sharply pointed spines; fourth tarsomeres subcylindrical; claws equal in ♂, equal or unequal in ♀; ♀ claws (Figs 204–205) with long inner basal teeth. Wing (Fig. 206) with two long radial cells, costal ratio more than 0,75; media petiolate to barely sessile, the fork arising near r–m crossvein. ♀ abdomen with sternum 8 forming a subtriangular genital plate; one spermatheca. ♂ genitalia (Fig. 207) bulbous, directed ventrally under tip of abdomen; ninth tergum reduced and narrowed by broad fusion of the bulbous basistyles; parameres (Fig. 208) usually separate.

Immature stages: Undescribed.

Biology: *Echinohelea pastoriana* was reared from soil rich in organic matter from near very wet rocks, from mud at a pond margin, and mud in the bottom of a drain; *E. vicina* Clastrier was reared from soil at the margin of a 'marigot'.

Distribution: Pantropical to subtemperate; 22 species.

Afrotropical species:
harbelensis de Meillon, 1960: 409. Liberia.
ornata Clastrier, 1984*b*: 368. Rep. Guinea.
pastoriana Clastrier, 1984*b*: 362. Rep. Guinea.
vicina Clastrier, 1984*b*: 366. Rep. Guinea.
voltana de Meillon, 1959*b*: 15. Upper Volta.

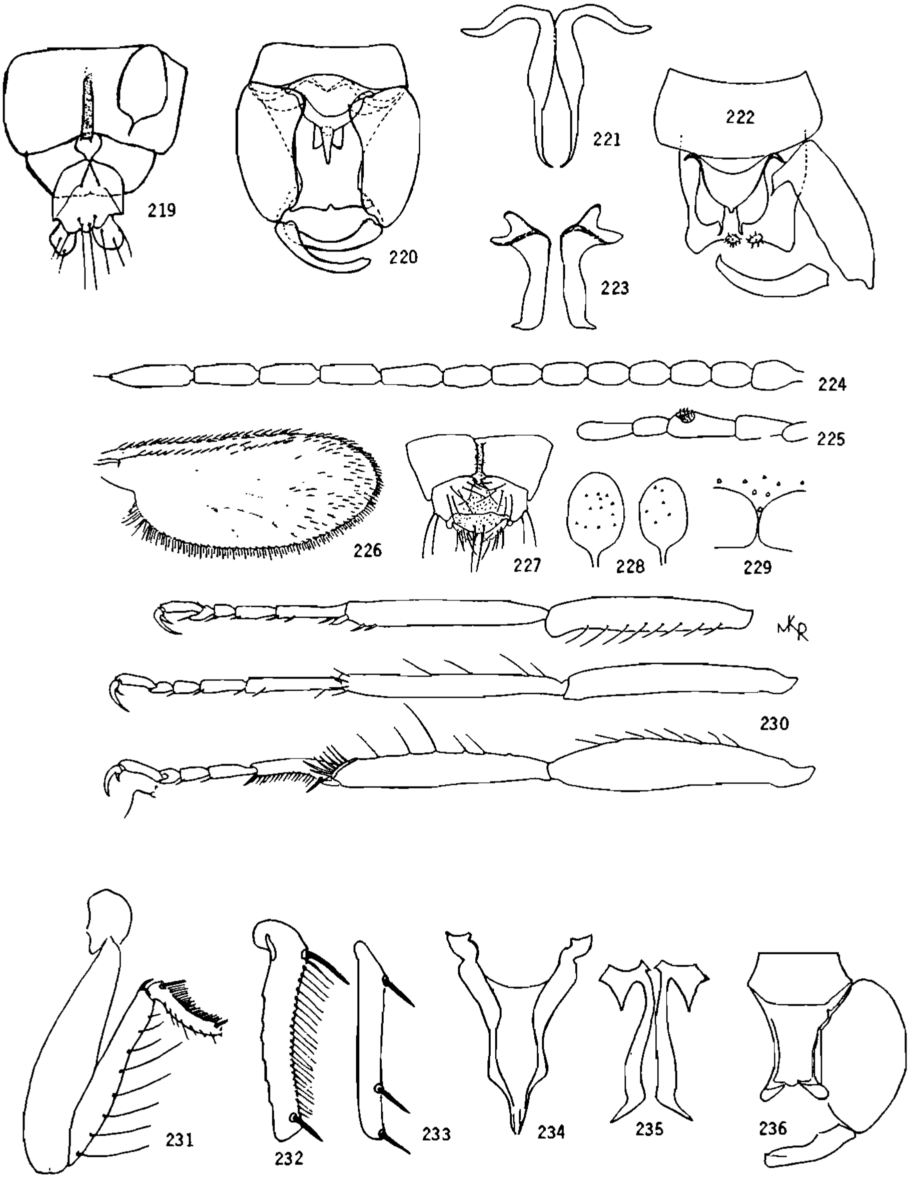
Genus *Fanthamia* de Meillon

(Figs 211–223)

Ceratopogon, subgenus *Fanthamia* de Meillon, 1939*b*: 103. Type species, *Ceratopogon adulator* de Meillon, by original designation.

References: De Meillon & Wirth, 1979*c*: 191 (revision); de Meillon & Downes, 1986: 165 (key to ♂).

Diagnosis: Small midges, wing length 0,7–0,9 mm. Eyes broadly separated, usually bare. Antenna (Fig. 212) with sensilla coeloconica present on segments 11–14 in both sexes; ♂ flagellum (Fig. 213) without plume, segments not fused, last five segments elongated as in ♀. Palpus (Fig. 215) 5-segmented, stubby; third segment swollen, with or without sensory pit. Mandible as in Fig. 214. Legs moderately slender, hind femur and tibia swollen in some species; femora unarmed; fourth tarsomeres cordiform; ♀ claws without basal inner tooth, small and equal on fore and mid legs, large and unequal on hind legs (small and equal on all legs in *imperfectus*) (Fig. 218). Wing (Fig. 211) often with faint to conspicuous colour pattern of large areas of coarse dark microtrichia; first radial cell complete,



Figs 219–236. Tribe Ceratopogonini: 219–221, *Fanthamia cardinis*; 222–223, *Fanthamia jonkeri* de Meillon & Wirth; 224–236, *Kolenohelea dycei* de Meillon & Wirth; 219, 227, female genitalia; 220, 222, male genitalia, parameres omitted; 221, 223, 235, male parameres; 224, female antenna; 225 female palpus; 226, female wing; 228, female spermathecae; 229, female eye separation; 230, female legs; 231, male hind leg, femur, tibia, basitarsus; 232, male hind basitarsus; 233, male fore basitarsus; 234, male aedeagus; 236, male ninth segment, basistyle, dististyle.

second obliterated; macrotrichia usually numerous; costal ratio about 0,6. ♀ with two spermathecae (Fig. 217); an internal sclerotisation sometimes present just posterior to sternum 9 (Fig. 219). ♂ genitalia (Figs 220, 222) with ninth tergum narrowed on distal half, without apicolateral processes; aedeagus with low basal arch and long slender distal process; parameres (Figs 221, 223) separate, each a nearly straight, tapering process arising from a stout anterolateral apodeme.

Immature stages and Biology: Unknown.

Distribution: Afrotropical Region; 14 species.

Included species:
abditus de Meillon & Wirth, 1987*a*: 46. South Africa.
adulator de Meillon, 1939*b*: 104 (*Ceratopogon*). South Africa.
aniculae de Meillon & Downes, 1986: 167. South Africa.
cardinis de Meillon & Wirth, 1979*c*: 194. South Africa.
carina de Meillon & Hardy, 1953: 28 (*Ceratopogon*). South Africa.
draconis de Meillon & Downes, 1986: 170. South Africa.
forsteri de Meillon & Downes, 1986: 169. South Africa.
gigantulus de Meillon & Wirth, 1979*c*: 196. South Africa.
imperfectus Goetghebuer, 1935: 172 (*Culicoides*). Zaïre.
jonkeri de Meillon & Wirth, 1987*a*: 48. South Africa.
mennoi de Meillon & Wirth, 1981*c*: 582. South Africa.
montana de Meillon & Downes, 1986: 167. South Africa.
ornatipennis de Meillon, 1939*b*: 106 (*Ceratopogon*). South Africa.
sani de Meillon & Downes, 1986: 168. South Africa.

Genus *Kolenohelea* de Meillon & Wirth

(Figs 224–236)

Kolenohelea de Meillon & Wirth, 1981*a*: 513. Type species, *Kolenohelea dycei* de Meillon & Wirth, by original designation.

Diagnosis: Medium size, stout, dark brown species; wing length 1,2–1,5 mm. Eyes contiguous in ♀, variably separated in ♂; bare. Antenna (Fig. 224) moderately elongate; in ♂ with well-developed plume, segments 4–11 fused. Palpus (Fig. 225) 5-segmented. Legs (Fig. 230) stout, hind femur conspicuously swollen; femora unarmed; tarsomeres 1–3 armed with some stout black ventral spines (Figs 230–233); fourth tarsomeres (Fig. 230) cordiform and bearing ventrally at apex a pair of whip-like hyaline sensilla. ♀ claws resembling those of *Stilobezzia*, appearing as a single long talon with a strong basal tooth; fifth tarsomeres without batonnets (Figs 230). Wing with two radial cells, first narrow and not rhomboidal as in *Stilobezzia* (Fig. 226); costal ratio 0,76. ♀ with one or two (Fig. 228) oval spermathecae; genital sclerotisation as in Fig. 227. ♂ genitalia (Fig. 236) with swollen basistyle and rather long ninth sternum; ninth tergum with tip modified into more or less elongate apicolateral processes; dististyle modified according to species; aedeagus (Fig. 234) a stout tapering sclerite with low basal arch, tip slender and pointed; parameres (Fig. 235) separate, similar to those of *Stilobezzia*, with long basal apodeme, more or less rod-like main body and tip obliquely truncated, tapered or hooked.

Immature stages and Biology: Unknown.

Distribution: Southern Africa and Europe; 17 species.

Afrotropical species:
dycei de Meillon & Wirth, 1981*a*: 517. South Africa.
equilis de Meillon & Wirth, 1987*a*: 48. South Africa.
fuscipennis Clastrier, 1984*a*: 369. Rep. Guinea.
inusitata de Meillon & Wirth, 1981*c*: 586. South Africa.
jarmilae de Meillon & Downes, 1986: 172. South Africa.
kindiae Clastrier, 1984*a*: 366. Rep. Guinea.
leonina de Meillon & Wirth, 1987*a*: 50. South Africa.
milleri de Meillon & Wirth, 1981*a*: 521. South Africa.
mira de Meillon & Wirth, 1981*c*: 583. South Africa.
mirabunda de Meillon & Wirth, 1981*a*: 522. South Africa.
mirifica de Meillon & Wirth, 1981*a*: 519. South Africa.
monticola de Meillon & Downes, 1986: 174. South Africa.
ornata Clastrier, 1984*a*: 367. Rep. Guinea.
pedi de Meillon & Wirth, 1987*a*: 50. South Africa.
pugilator de Meillon & Wirth, 1987*a*: 52. South Africa.
uysorum de Meillon, Meiswinkel & Wirth, 1982: 138. South Africa.

Genus *Luciamyia* de Meillon

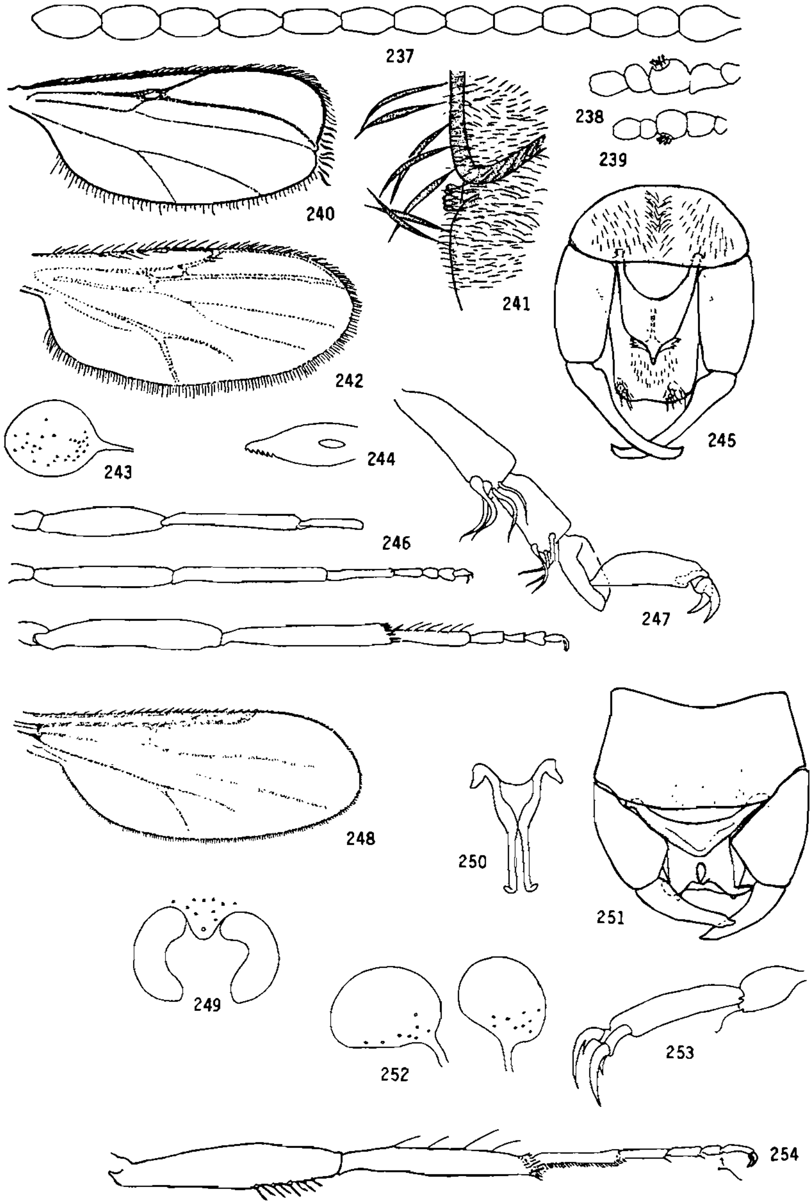
(Figs 237–247)

Luciamyia de Meillon, 1937: 380. Type species, *Luciamyia biloba* de Meillon, by original designation.

Diagnosis: A medium size brownish midge; wing length 1,4 mm. Eyes contiguous, bare. Antenna (Fig. 237) short; ♂ antenna without plume, last five segments as in ♀. Palpus (Figs 238–239) short, third segment short with broad shallow sensory pit. ♀ mandible as in Fig. 244. Legs (Fig. 246) slender; femora unarmed; femora and tibiae with numerous long bristly setae; fourth tarsomeres cordiform; fifth tarsomeres slender, unarmed; in ♂ tarsomere 2 of mid and hind legs and tarsomere 3 of hind leg each with ventral clump of stout, strongly bent, colourless spines (Fig. 247). Claws short and simple on all legs in both sexes (Fig. 246). Wing with dense, sharp-pointed microsetae in both sexes; two radial cells; in ♂ (Fig. 242) first small, second long, extending nearly to wing tip; in ♀ (Fig. 240) costa extending to apex of wing where it meets tips of veins R4 + 5 and M1 in an indentation of wing margin, a small sclerotisation and some scales at the junction (Fig. 241), second radial cell thus usually broad distally; vein M2 absent in ♀, in ♂ complete and media with long petiole. One spermatheca (Fig. 243). ♂ genitalia (Fig. 245) with ninth tergum narrow, without apicolateral processes; aedeagus with well-sclerotised distal process flanked by several pointed lateral processes; parameres with V-shaped basal connective and a pair of arcuate bladelike sclerites.

Immature stages and Biology: Unknown.

Distribution: South Africa; 1 species.



Figs 237–254. Tribe Ceratopogonini: 237–247, *Luciamyia biloba* de Meillon; 248–254, *Metacanthohelea cogani* Wirth & Grogan; 237, female antenna; 238, female palpus; 239, male palpus; 240, 248, female wing; 241, apex female wing; 242, male wing; 243, 252, female spermatheca(e); 244, female mandible; 245, 251, male genitalia, parameres omitted; 246, female legs (partial); 247, female hind leg, tarsomeres 2–5; 249, female eye separation; 250, male parameres; 253, female hind leg, tasomeres 4–5; 254, female hind leg.

Included species:
biloba de Meillon, 1937: 380. South Africa.
irrita de Meillon, 1937: 383 (*Monohelea*). South Africa; synonym of *biloba*.

Genus *Metacanthohelea* Wirth & Grogan

(Figs 248–254)

Metacanthohelea Wirth & Grogan, 1988: 65. Type species, *Metacanthohelea cogani* Wirth & Grogan, by original designation.

Diagnosis: Small, dull dark brown midges; wing length 0,90 mm. Eyes (Fig. 249) broadly separated, bare. ♀ antenna with distal five segments elongated; ♂ with distal three segments elongated, segments 3–10 fused, with sparse plume. Palpus 5-segmented; third segment short, swollen, with well-defined pit. Legs moderately stout; hind femur (Fig. 254) swollen, bearing 14 large ventral spines on distal half; fourth tarsomeres (Fig. 253) short but subcylindrical, bearing single apical sinuate hyaline sensillum; ♀ claws small and equal, distinctly curved near base, with basal inner teeth. Wing (Fig. 248) milky, with two narrow radial cells, second 1,5 times length of first; costal ratio 0,67; vein M2 narrowly interrupted at base. Two ovoid spermathecae (Fig. 252) with oblique long slender necks. ♂ aedeagus (Fig. 251) triangular, broad and short; parameres (Fig. 250) fused basally with long slender distal portions recurved at their tips.

Immature stages and Biology: Unknown.

Distribution: Aldabra Atoll; Kenya.

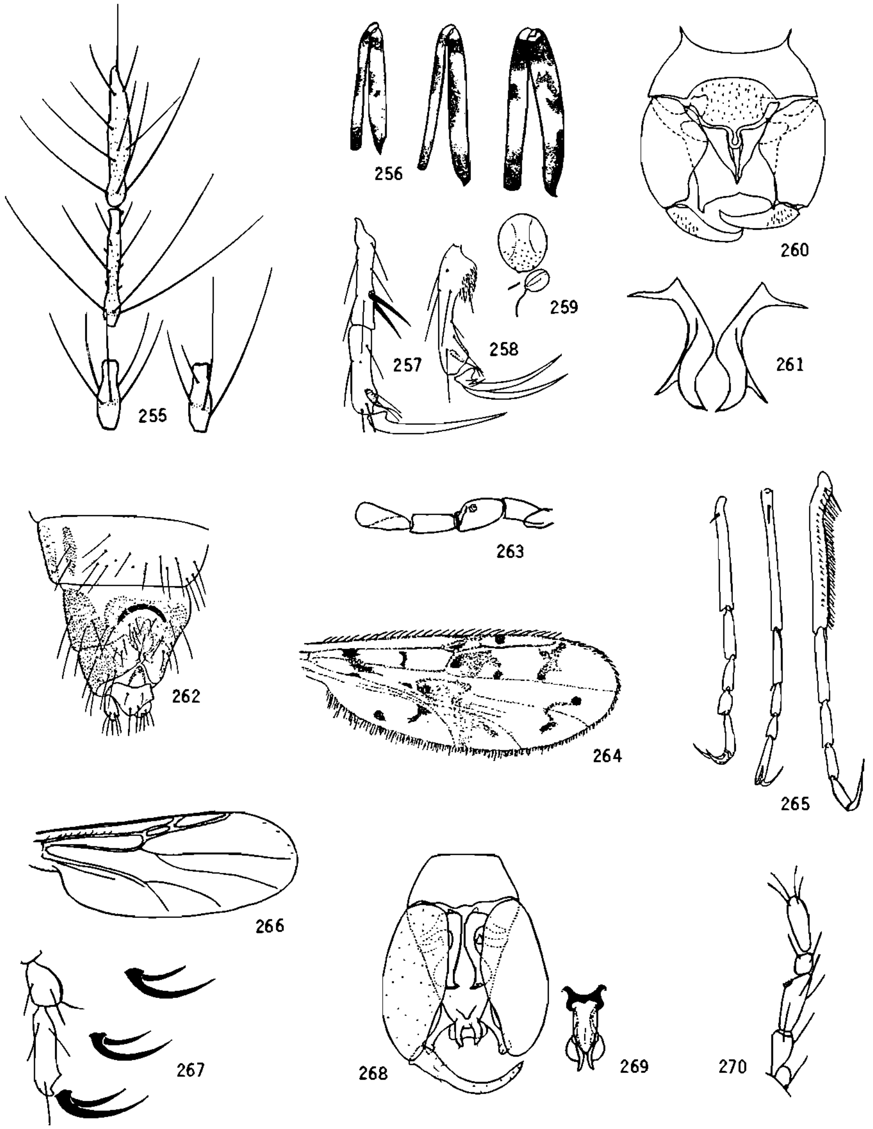
Included species:
cogani Wirth & Grogan, 1988: 66. Aldabra Atoll; Kenya.

Genus *Monohelea* Kieffer

(Figs 255–265)

Monohelea Kieffer, 1917*b*: 294. Type species, *Monohelea hieroglyphica* Kieffer, by original designation.

Diagnosis: Small to medium size species with yellowish brown body and with conspicuous hieroglyphic pattern or dark markings on wing (Fig. 264); wing length 1–2 mm. Legs (Fig. 256) usually yellowish with dark brown rings or bands. Eyes contiguous, bare. Antenna (Fig. 255) variable in length; ♂ with plume, flagellar segments not fused. Palpus (Fig. 263) 5-segmented; third segment slender to moderately stout. Fore and mid legs slender, hind femur and tibia somewhat thickened but without spines; fourth tarsomeres cylindrical, elongated on hind leg (Fig. 265); fore and mid fifth tarsomeres swollen basoventrally (Fig. 258); ♀ claws of fore and mid legs equal, large, curved, with basal inner and outer teeth (Fig. 258); hind leg with one very long talon without basal tooth (Fig. 257); ♂ claws small and equal on all legs. Wing (Fig. 264) with two radial cells, second longer than first, the two separated by a short fusion of the veins between them; costal ratio 0,7 or more. ♀ with two spermathecae, unequal to greatly unequal, the smaller one usually with fine thread-like sclerotisation of the duct (Fig. 259). ♂ aedeagus (Fig. 260) with sclerotised basal loop, a pair of sharp-pointed,



Figs 255–270. Tribe Ceratopogonini: 255–259, 262, *Monohelea legrandi* Clastrier; 260–261, 263–265, *Monohelea hieroglyphica* Kieffer; 266–270, *Neohelea pastoriana* Clastrier; 255, female antenna; 256, female femora and tibiae; 257, female hind leg, tarsomeres 4–5; 258, female fore leg, tarsomere 5; 259, spermathecae; 260, 268, male genitalia; 261, male parameres; 262, female genitalia; 263, 270, female palpus; 264, 266, female wing; 265, female tarsi; 267, female claws; 269, male aedeagus.

tapered lateral sclerites and an accessory dorsomedian posterior lobe; parameres (Fig. 261) consisting of paired submedian sclerites of various shapes, sometimes joined proximally.

Immature stages: Larva with head suboval, 1,8 times as long as broad, slightly flattened dorsoventrally, slightly tapering anteriorly; epipharynx with one pair of combs; hypopharynx conical; anal segment with eight stout black setae, their length less than that of segment. Pupa (of *M. hirsuta* Wirth & Grogan) stout and tapering, with well-developed dorsal tubercles; respiratory horn short and stout, broader at base, apex with about eight spiracular openings.

Biology: North American species have been reared from sphagnum moss (Wirth & Grogan, 1981).

Distribution: Worldwide; 64 species.

Afrotropical species:
andrei Vattier & Adam, 1966*b*: 744. Rep. Congo.
chalybeata Clastrier, 1960*a*: 286. Rep. Congo.
cognata Clastrier, 1960*a*: 289. Congo.
legrandi Clastrier, 1984*c*: 49. Gabon.
periucunda de Meillon & Wirth, 1981*c*: 587. South Africa.
polychroma Clastrier, 1958: 252. Senegal.
praeclara Goetghebuer, 1935: 178. Zaïre.
transversalis Clastrier, 1960*a*: 290. Rep. Congo.

Genus *Neohelea* Clastrier

(Figs 266–270)

Neohelea Clastrier, 1988*b*: 53. Type species, *Neohelea pastoriana* Clastrier, by original designation.

Diagnosis: Small blackish midges with unmarked wings; wing length 0,87 mm. Eyes broadly separated, with short pubescence. Antenna with sensilla coeloconica on segments 11–14 of ♀, on 14 of ♂; in ♂ with plume. Palpus (Fig. 270) 5-segmented; third segment with small round sensory pit. Legs slender, femora not swollen, unarmed; hind basitarsus with strong basal spine; fourth tarsomeres (Fig. 267) stout but not cordiform, with a pair of slightly bent hyaline sensilla; fifth tarsomeres unarmed; ♀ claws (Fig. 267) similar on all legs, long, slender and curved, slightly unequal, without basal tooth. Wing (Fig. 266) with two well-formed radial cells; costal ratio 0,75 in ♀, 0,65 in ♂; media with short petiole, vein M2 complete to base; a few macrotrichia at wing tip in ♀. ♀ with two subequal ovoid spermathecae with short wide necks. ♂ genitalia (Fig. 268) elongate, ninth tergum markedly tapering distally with long, digitiform apicolateral processes; dististyle slender, bent hooklike; aedeagus (Fig. 269) small and laterally compressed, narrow in ventral view, with short basal arch, a pair of slender distal processes and rounded, subapical, lateral flanges; parameres separate, short and stout, sinuate with blunt-pointed, ventrally bent tips.

Immature stages and Biology: Unknown.

Distribution: Rep. Guinea; 1 species.

Included species:
pastoriana Clastrier, 1988*b*: 55. Rep. Guinea.

Genus *Notoceratopogon* de Meillon & Downes
(Figs 271–279)

Notoceratopogon de Meillon & Downes, 1986: 157. Type species, *Notoceratopogon minutus* de Meillon & Downes, by original designation.

Diagnosis: Small to medium size brownish midges with pale unadorned wings; wing length 0,6–1,8 mm. Eyes narrowly separated, pubescent. Antenna of ♀ with sensilla coeloconica on segments 12–14; in ♂ (Fig. 272) segments 4–12 fused, last three segments elongated, plume well developed. Palpus 5-segmented. Legs slender, femora not swollen, unarmed; fourth tarsomeres cordiform, with a pair of simple, downwardly bent, hyaline sensilla; ♀ claws small and equal, each with short basal inner tooth (Fig. 273); small empodium present. Wing (Fig. 271) with costa short, costal ratio 0,45–0,50; radial cells small and subequal, separated by approximation of upper and lower veins rather than by definite vein R2+3. ♀ with two spermathecae (Fig. 274) plus vestigial third, walls very irregular, not smoothly curving. ♂ ninth tergum (Fig. 275) with apicolateral processes projecting as slender cylindrical structures ending in a ring surrounding sunken base of apical seta; lateral margins of tergum inflected ventrally to form tongue-like processes directed mesally; dististyle as in Fig. 276; aedeagus (Figs 278–279) complex, generally a wide plate borne on strong basal arms and sometimes with median thickening, and a pair of elongate structures from anterior margin and crossing beneath main plate; parameres (Figs 277–278) short but strong, separate, shaft broadly united with short, strong basal apodeme, one or two short hook-shaped prongs at end near tip.

Immature stages and Biology: Unknown.

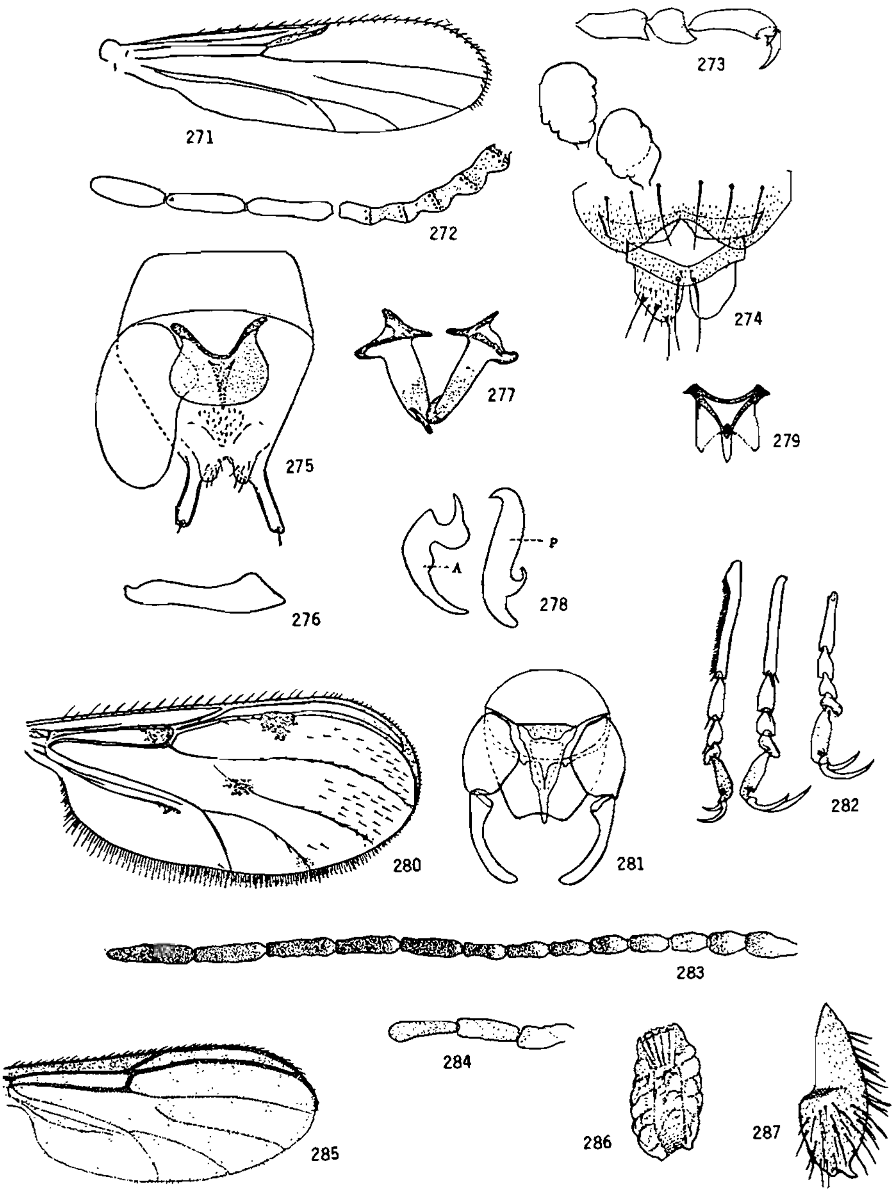
Distribution: South Africa; 4 species.

Included species:
alcides de Meillon & Hardy, 1954: 74 (*Ceratopogon*). South Africa.
minutus de Meillon & Downes, 1986: 161. South Africa.
natalensis de Meillon, 1937: 378 (*Ceratopogon*). South Africa.
vockerothi de Meillon & Downes, 1986: 162. South Africa.

Genus *Parabezzia* Malloch
(Figs 281–287)

Parabezzia Malloch, 1915: 358. Type species, *Parabezzia petiolata* Malloch, by original designation.

Diagnosis: Moderately small, stout midges, wing length 0,9–1,3 mm. Eyes moderately separated, bare. Antenna (Fig. 283) moderately long; ♂ with well-developed plume, proximal segments not fused. Palpus (Fig. 284) 4-segmented, slender, without sensory pit. Legs slender, unarmed; ♂ fore and mid coxae with dense long spine-like bristles (Fig. 287); fourth tarsomeres cordiform; fifth tarsomeres stout and laterally compressed, sometimes swollen or tuberculate



Figs 271–287. Tribe Ceratopogonini: 271–272, 275–278, *Notoceratopogon natalensis* (de Meillon); 273–274, 279, *Notoceratopogon vockerothi* de Meillon & Downes; 280, *Paralluaudomyia maculata* Clastrier; 281–287, *Parabezzia eupetiolata* Grogan & Wirth; 271, male wing; 272, male antennal segments 8–15; 273, female tarsomeres 3–5; 274, female genitalia and spermathecae; 275, male genitalia, parameres omitted; 276, male diststyle; 277, male parameres; 278, male aedeagus and parameres, side view; 279, male aedeagus; 280, 285, female wing; 281, male genitalia; 282, female tarsi; 283, female antenna; 284, female palpus; 286, pupal respiratory horn; 287, male fore coxa.

ventrally; ♀ claws long and curved, equal or unequal, without basal inner teeth (Fig. 282); ♂ claws small and equal. Wing (Fig. 285) broad in ♀; macrotrichia absent; one radial cell, elongate in ♀ with costa prolonged to or near wing tip, reaching halfway between apices of veins R4 + 5 and M1, ♂ costa ending at 0,6 of wing length; costa often with a bead-like or scale-like swelling at base near basal arculus. Two spermathecae without distinct necks. ♂ genitalia (Fig. 281) short and broad; tergum rounded distally; aedeagus large and triangular; parameres fused in a small, pointed, triangular, hyaline sclerite hidden in ventral view by the aedeagus.

Immature stages: Larva unknown. Pupa (after Wirth & Grogan 1981: 49) short and compact; body with prominent rounded tubercles; caudal processes of abdomen short and conical, sharp pointed; respiratory horn (Fig. 286) short and stout, scarcely twice as long as broad, with truncated tip bearing distal row of 6–10 spiracular openings.

Biology: *Parabezzia stagni* was reared from a ground water pool at Doornpan, Bulge River, by Alan Dyce.

Distribution: Western Hemisphere, Africa, Sri Lanka; 30 species.

Afrotropical species:
falcipennis Clastrier, 1960*a*: 293. Rep. Congo.
insolita Vattier & Adam, 1966*b*: 769. Rep. Congo. Synonym of *falcipennis* Clastrier.
obscura de Meillon & Wirth, 1981*c*: 588. South Africa.
stagni de Meillon & Wirth, 1981*b*: 538. South Africa.

Genus *Paralluaudomyia* Clastrier

(Fig. 280)

Paralluaudomyia Clastrier, 1960*a*: 268. Type species, *Paralluaudomyia maculata* Clastrier, by original designation.

Diagnosis: ♀ only known. As in *Alluaudomyia*, but radial cell long, extending to wing tip; costa nearly attaining apex of vein M1 (Fig. 280).

Distribution: Rep. Congo; 1 species.

Included species:
maculata Clastrier, 1960*a*: 268. Rep. Congo.

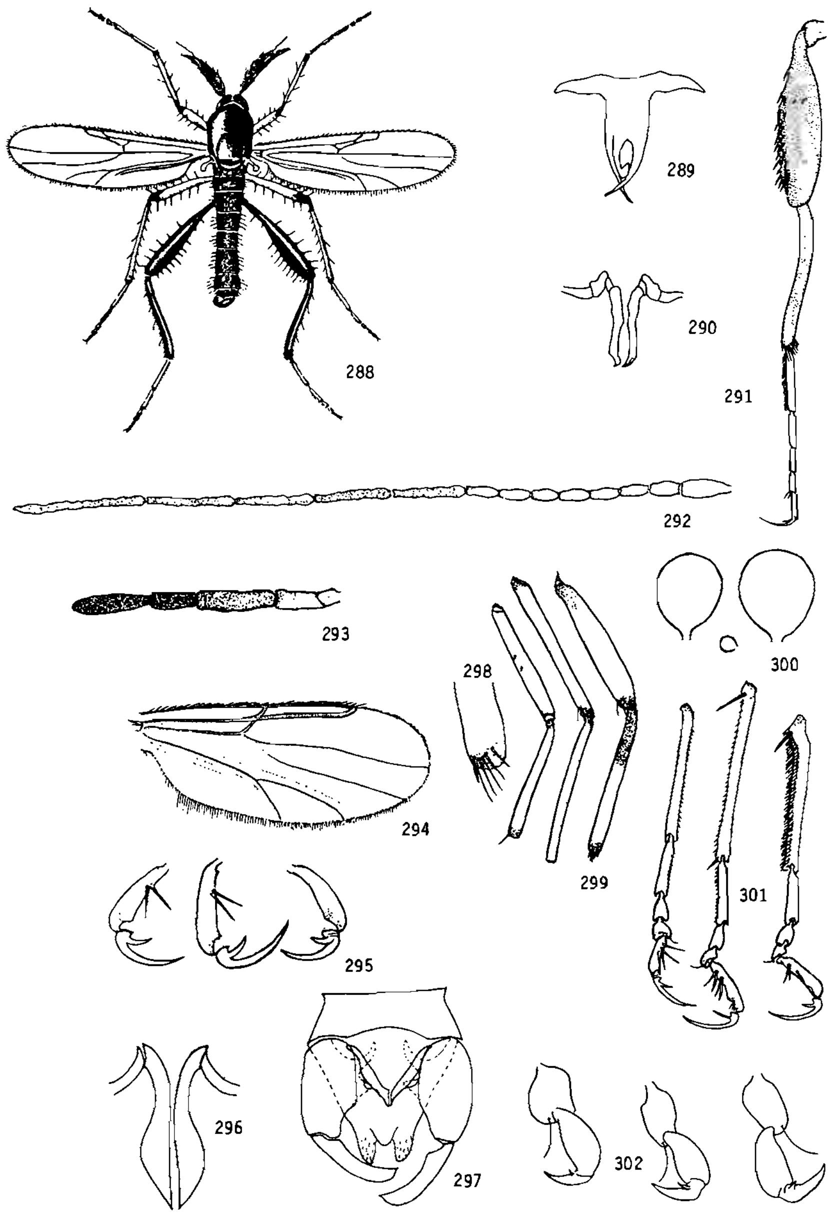
Genus *Serromyia* Meigen

(Figs 288–291)

Serromyia Meigen, 1818: 83. Type species, *Ceratopogon femoratus* Meigen, by monotypy.

Reference: De Meillon & Wirth, 1983*b*: 383 (revision Afrotropical species).

Diagnosis: Moderately large, stout-bodied midges (Fig. 288); wing length 1,0–2,5 mm. Eyes bare, contiguous to moderately separated. ♂ antenna with separate or partially fused segments and well-developed plume. Palpus 5-segmented; third segment with or without sensory pit. Fore and mid legs slender and



Figs 288–302. Tribe Ceratopogonini: 288, *Serromyia femorata* (Meigen); 289–291, *Serromyia stuckenbergi* de Meillon & Wirth; 292–293, 295, *Stilobezzia (Stilobezzia) festiva* Kieffer; 294, 298–301, *Stilobezzia (Eukraiohelea) elegantula* (Johannsen); 296–297, *Stilobezzia (Acanthohelea) lutea* (Malloch); 302, *Stiloculicoides ugandae* (Ingram & Macfie); 288, male habitus; 289, male aedeagus; 290, 296, male parameres;291, female hind leg; 292, female antenna; 293, female palpus; 294, female wing; 295. female fifth tarsomeres; 297, male genitalia, parameres omitted; 298, hind tibial comb; 299, female femora and tibiae; 300, female spermathecae; 301, female tarsi; 302, female tarsomeres 4–5.

unarmed, hind femur (Fig. 291) greatly swollen and armed ventrally with numerous stout spines, usually in two series; hind tibia (Fig. 291) slender and arcuate to fit against femur; fourth tarsomeres on fore and mid legs subcylindrical, elongate on hind leg; claws of fore and mid legs simple and equal, nearly straight, each with inner basal tooth; hind claw of ♀ usually a single long talon with sharp basal tooth of variable length and thickness, rarely with a pair of small equal claws (Fig. 291). Wing (Fig. 288) usually without colour pattern; costal ratio 0,52–0,85 in ♀, 0,41–0,73 in ♂; two more or less equal size, narrow radial cells; media subsessile to petiolate. One or two spermathecae. ♂ aedeagus (Fig. 290) short with broad basal arch, distomedian process varies according to species; parameres (Fig. 291) usually a pair of simple elbowed or gently bent sclerites with short, broad, basal apodemes, sometimes narrowly fused.

Immature stages: Larval head small and tapering anteriorly; epipharynx with two combs; perianal setae inconspicuous. Pupa with respiratory horn short, with 8–11 spiracular openings on prominences at tip and around distal third.

Biology: Larvae have been found in damp moss and in marshlands in Europe; they are non-swimming and crawl slowly (Kettle & Lawson, 1952).

Distribution: Worldwide except Neotropical; 40 species, including 8 as fossil species.

Afrotropical species:
aethiopiae Clastrier & Wirth, 1961*a*: 219. Gambia.
agathae de Meillon & Wirth, 1983*b*: 388. South Africa.
festiva Kieffer, 1911*b*: 346. Seychelles.
meiswinkeli de Meillon & Wirth, 1983*b*: 390. South Africa.
neethlingi de Meillon & Wirth, 1983*b*: 392. South Africa.
nocticolor Kieffer, 1914: 268. South Africa.
rossi de Meillon & Wirth, 1983*b*: 396. Madagascar.
silvatica de Meillon & Downes, 1986: 175. South Africa.
stuckenbergi de Meillon & Wirth, 1983*b*: 398. South Africa.
zuluensis de Meillon & Wirth, 1981*c*: 589. South Africa.

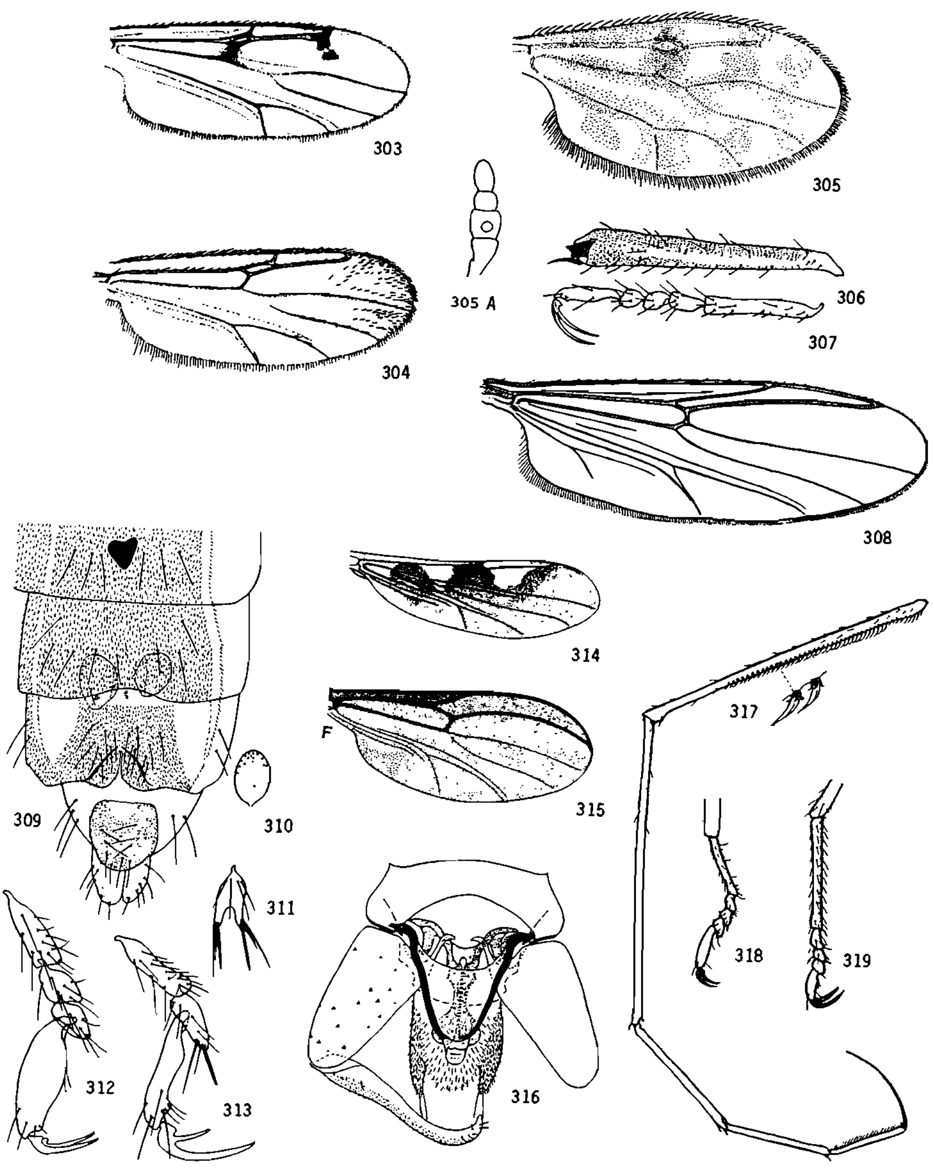
Genus *Stilobezzia* Kieffer

(Figs 292–301, 303–304)

Synonymy under subgeneric headings.

Reference: Clastrier, 1976: 567 (taxonomic analysis of subgenera and species groups for world).

Diagnosis: Small to moderately large, slender midges. Eyes bare, narrowly to broadly separated. Antenna (Fig. 292) usually long and slender; ♂ antenna with plume. Palpus (Fig. 293) 5-segmented. Legs (Fig. 299) slender; femora usually unarmed, rarely with ventral spines on fore leg; fourth tarsomeres (Fig. 301) cordiform or bilobed, sometimes the lobes armed with spines; fifth tarsomeres in ♀ unarmed (as in ♂) or armed with strong spines or batonnets; claws (Fig. 295) of ♀ reduced to a single long talon with a short basal tooth, lengths of the talons similar or dissimilar on the three pairs of legs; ♂ claws usually small and equal. Wing (Figs 294, 303–304) with or without macrotrichia; two radial cells present



Figs 303–319. Tribes Ceratopogonini and Heteromyiini: 303, *Stilobezzia festiva*; 304, *Stilobezzia lutea*; 305–305A, *Stiloculicoides ugandae*; 306–307, 315, *Neurobezzia tsacasi* Clastrier; 308, 317–319, *Pellucidomyia ugandae* Macfie; 309–313, *Clinohelea hygropetrica* Clastrier; 314, 316, *Clinohelea trimaculata* Clastrier; 303–305, 308, 314–315, female wing; 305A, female palpus; 306, female fore tibia; 307, 318, female fore tarsus; 309, female abdomen, posterior segments; 310, spermatheca; 311, female hind leg, tarsomere 4; 312, female fore leg, tarsomeres 2–5; 313, female hind leg, tarsomeres 3–5; 316, male genitalia; 317, female hind tarsus; 319, female mid tarsus.

except in subgenus *Eukraiohelea*, the first usually of distinctly rhomboid or parallelogram shape; costa extending to 2/3 or more of wing length; vein R1 located in direct line with r–m crossvein; media usually with long petiole. ♀ with two spermathecae (Fig. 300), rarely three or one. ♂ genitalia (Fig. 297) with basistyle stout, usually with mediangular or basidorsal process or mesal connective bridge; aedeagus membranous with pair of oblique lateral sclerites; parameres (Fig. 296) usually separate, slender and bladelike, with slender basal apodeme.

Immature stages: Larva with dark brown head and whitish body; head tapering anteriorly, about twice as long as broad; epipharynx with two combs. Pupa relatively slender, smooth, without strongly developed dorsal tubercles or processes; respiratory horn usually elongate and nearly straight, surface smooth, with several lateral spiracular openings and a row of distal openings; terminal processes of abdomen usually sharp-pointed and diverging laterally.

Biology: Females are predaceous on other small, soft bodied insects. Larvae are found in a wide variety of aquatic and semi-aquatic habitats, which in Africa include stream, lake and pond margins, puddles, swamps, rice fields, rock pools, and wet tree cavities. Larval habitats have been recorded for 17 Afrotropical species.

Subgenus *Stilobezzia* Kieffer

(Figs 292–293, 295, 303)

Stilobezzia Kieffer, 1911*a*: 118. Type species, *Stilobezzia festiva* Kieffer, by original designation.

Diagnosis: Wing (Fig. 303) without macrotrichia, sometimes with pattern of small to moderately large dark areas; first radial cell relatively small but distinct; second radial cell usually elongate and not very broad; stem of media usually 2–3 times length of r–m crossvein. Legs without stout spines on femora, setae poorly to moderately developed; fourth tarsomeres cordiform; fifth tarsomeres (Fig. 295) often with ventral batonnets. Abdomen usually with colour pattern dorsally, anterior terga often with striking ornamentation and setal clusters. ♂ parameres separate.

Distribution: Worldwide, more abundant in tropics; 138 species.

Afrotropical species: The Afrotropical Catalogue lists 21 species; additions and corrections:

angustipennis Clastrier, 1988*a*: 125. Rep. Guinea.
brevicornis Clastrier, 1988*a*: 130. Rep. Guinea.
crossi de Meillon & Wirth, 1981*c*: 591. South Africa.
mutabilis Clastrier, 1986*d*: 63. Rep. Guinea.
nyei Clastrier, 1983*c*: 77. Seychelles.
pallidipes Clastrier, 1983*c*: 78. Seychelles.
pastoriana Clastrier, 1986*d*: 66. Rep. Guinea.
paucimaculata Clastrier, 1984*d*: 46. Rep. Guinea.
photophila Clastrier, 1984*d*: 43. Rep. Guinea.
seychelleana Clastrier, 1983*c*: 79. Seychelles.

Subgenus *Acanthohelea* Kieffer

(Figs 296–297, 304)

Acanthohelea Kieffer, 1917*a*: 198. Type species, *Acanthohelea pruinosa* Kieffer, by monotypy.
Stilobezzia, subgenus *Neostilobezzia* Goetghebuer, in Goetghebuer & Lenz, 1934: 53. Type species, *Ceratopogon ochraceus* Winnertz, designated by Wirth, 1953: 63. Synomymy by Wirth & Grogan, 1988: 88.

Diagnosis: Moderately large species with yellowish to brownish colour and usually unmarked wings; legs with well-developed bristle-like setae. Wing (Fig. 304) bearing at least a few macrotrichia on the membrane; first radial cell spacious, usually subquadrangular; second radial cell large; petiole of media usually subequal in length to r–m crossvein. Legs without stout spines on femora, but setae frequently numerous and strong, especially on tibiae; fourth tarsomeres cordiform; fifth tarsomeres rarely with ventral spines or batonnets. Abdomen without prominent colour pattern on terga. Spermathecae one or two. ♂ genitalia (Fig. 297) with ninth tergum more elongate than in *Stilobezzia s. s.*; basistyle usually with only mediangular process present; parameres (Fig. 296) separate, basal sclerites usually bisinuate, with outer expansion at midlength, rarely with submedian caudal membranous accessory lobes present.

Distribution: Worldwide, more numerous in temperate regions; 127 species.

Afrotropical species: The Afrotropical Catalogue lists 13 species; additions and corrections:

amplistyla Clastrier, 1989: 13. Rep. Guinea.
brevistyla Clastrier, 1989: 12. Rep. Guinea.
carayoni Clastrier, 1986*c*: 284. Rep. Guinea.
donskoffi Clastrier, 1988*b*: 60. Zaïre.
djalonensis Clastrier, 1988*a*: 127. Rep. Guinea.
flavida de Meillon & Wirth, 1987*a*: 56. South Africa.
fulva de Meillon & Downes, 1986: 176. South Africa.
gigantiforceps Clastrier, 1989: 6. Rep. Guinea.
insigniforceps Clastrier, 1989: 9. Rep. Guinea.
kindiae Clastrier, 1988*a*: 121. Rep. Guinea.
latistyla Clastrier, 1989: 10. Rep. Guinea.
latiunguis Clastrier, 1985: 460. Rep. Guinea.
orientis de Meillon & Wirth, 1981*b*: 541. South Africa.
ornatithorax Clastrier, 1988*a*: 128. Rep. Guinea.
singularis Clastrier, 1985: 464. Rep. Guinea.
trimaculata de Meillon & Wirth, 1987*a*: 57. South Africa.
unicellula Clastrier, 1985: 463. Rep. Guinea.

Subgenus *Eukraiohelea* Ingram & Macfie

(Figs 294, 298–301)

Eukraiohelea Ingram & Macfie, 1921: 347. Type species, *Eukraiohelea africana* Ingram & Macfie, designated by Macfie, 1940*a*: 22.

Diagnosis: Usually small to medium size midges, greenish yellow to yellowish brown in colour. Wing (Fig. 294) without colour pattern; macrotrichia absent;

first radial cell obliterated and vein Rl arising at or past r–m crossvein; petiole of media long. Legs (Fig. 299) usually with weak setae; fore femur with 2–4 short stout spines midventrally in *africana* Group; fourth tarsomeres cordiform; fifth tarsomeres with or without batonnets; ♀ claws long, similar on all legs (Fig. 301); ♂ claws large and unequal. Abdomen patterned, with weak setae on terga. ♂ genitalia with mediangular processes of basistyles connected by a transverse sclerotised band or bridge, basidorsal process not developed; parameres separate, usually elongate.

Distribution: Worldwide except Australasian Region; 15 species.

Afrotropical species:
africana Ingram & Macfie, 1921: 347 (*Eukraiohelea*). Ghana.
foyi Ingram & Macfie, 1922: 270 (*Eukraiohelea*). Nigeria.
versicolor Ingram & Macfie, 1921: 351 (*Eukraiohelea*). Ghana.

Genus *Stiloculicoides* Wirth & Grogan
(Figs 302, 305, 305A)

Stiloculicoides Wirth & Grogan, 1988: 95. Type species, *Stilobezzia ugandae* Ingram & Macfie, by original designation.

Diagnosis: Small slender midges; wing length 1,0 mm. Eyes moderately separated, bare. Antenna slender in ♀; in ♂ last five segments elongated and plume absent. Palpus (Fig. 305A) stumpy, 5-segmented; third segment with small, round, shallow sensory pit. Wing (Fig. 305) short and broad; dark brown with prominent pattern of rounded pale spots in *Culicoides*-like arrangement; microtrichia coarse giving rise to the wing pattern, macrotrichia absent; two radial cells, first minute to small and diamond-shaped, second long and broad; r–m crossvein long and nearly perpendicular, nearly in line with Rl; costal ratio 0,77; media with long petiole. Legs short and stout, femora unarmed; basitarsi long, longer than distal tarsomeres combined; fourth tarsomeres weakly cordiform, apical hyaline sensilla slightly wavy distally; fifth tarsomeres short, without ventral batonnets; ♀ claws a single short talon on all legs, stout at base, slightly curved and distally pointed, with a small basal tooth (Fig. 302). ♀ abdomen short and stout, eighth and ninth segments forming a heavily sclerotised ring with ventromedian cleft and prominent pair of ventrolateral plates. No sclerotised spermatheca present. ♂ genitalia small; ninth sternum broad and produced posteriorly into basal arch of aedeagus; ninth tergum moderately long and caudally rounded; basistyle moderately elongate, simple; dististyle long and nearly straight, slightly tapered to blunt-pointed, hooked tip; aedeagus forming a slender rounded arch, distal process in form of an extremely short gutter open ventrally; parameres a pair of small apodemes dorsally at bases of basistyles.

Immature stages: Unknown.

Biology: Adults were reared from leaf mould at the base of a palm tree in Cameroun.

Distribution: Southern Africa; 1 species.

Included species:
ugandae Ingram & Macfie, 1923: 62 (*Stilobezzia*). Uganda.

Tribe Heteromyiini

Diagnosis: Large, nearly bare, predaceous midges. Antenna usually elongate, segments cylindrical in ♀. Palpus slender, 5-segmented. ♀ mandible with 7–10 coarse teeth. Mesonotum often with prominent anterior spine or tubercle. Legs long, usually slender, femora somewhat swollen distally, armed or unarmed; fourth tarsomeres (Fig. 311) cordiform, prolonged in bifid spinose lobes or greatly elongated (Fig. 317) on hind leg; fifth tarsomeres not armed with ventral spines or batonnets, those of fore leg (Fig. 312) often inflated, fusiform. Claws (Figs 307, 312–313, 317–319) of ♀ usually unequal, at least on hind leg, or a single claw with basal tooth. Wing (Figs 308, 314–315, 320) without macrotrichia, often fasciate or infuscated; fork of media barely to broadly sessile; one or two radial cells; costa extending to more than 0,7 of wing length. ♀ abdomen (Fig. 309) without eversible glands and sclerotised internal gland rods, often petiolate; two large sclerotised spermathecae usually present. ♂ genitalia (Fig. 316) usually long and slender; basistyle simple; dististyle long and slender; aedeagus simple, with basal arch low or high, distal portion short; parameres separated, slender, distal blades usually clavate.

Immature stages: Larval head with lateral arms of epicranial suture obsolescent on anterior half of head, thus resembling larvae of the tribes Sphaeromiini and Palpomyiini. Pupa without ventral membranous discs on abdominal segments.

Biology: Adult females are predaceous; immature stages are aquatic.

Genus *Clinohelea* Kieffer

(Figs 309–314, 316)

Clinohelea Kieffer, 1917*b*: 295. Type species, *Ceratopogon variegatus* Winnertz, by original designation.

Reference: According to Clastrier (1983*a*: 19) two Afrotropical species placed by Wirth *et al.* (1980) in the genus *Ceratobezzia* Kieffer in the Afrotropical Catalogue belong in the genus *Clinohelea*; *Ceratobezzia* is a Neotropical genus.

Diagnosis: Moderately large (wing length 1,5–3,2 mm), shining midges, usually with infuscated wing pattern (Fig. 314); thorax usually with transverse band of silvery pollinosity on pleura. Fourth tarsomere of at least mid and hind legs deeply bilobed, each lobe ending in a stout blunt spine and smaller spines (Fig. 311); fore fifth tarsomere (Fig. 312) greatly inflated in both sexes, often bicolored; fore claws of ♀ equal, mid and hind claws very unequal (Fig. 313). Wing with one or two radial cells. ♀ genitalia as in Fig. 309; spermathecae as in Fig. 310. ♂ aedeagus with low anterior arch, distal portion broad, underlying membrane extending beyond tip; parameres usually separate, each slender distally with elongated bulbous tip (Fig. 316).

Immature stages: Larvae are aquatic, swimming; larval mandibles especially long and slender, 1/3 as long as head; epipharynx with two pairs of well-developed combs and lateral arms each with comb of about ten strong teeth; anal segment and preanal segments subequal in length, former with four long and two short perianal setae. Pupa with respiratory horn moderately long and slender, about five times longer than broad, with about ten spiracular openings.

Biology: *Clinohelea hygropetrica* was reared from roots, moss and organic material in shallow rock pools; *C. trimaculata* was reared from the muddy margin of a rice paddy.

Distribution: Worldwide; 35 species.

Afrotropical species:
hygropetrica Clastrier, 1983*a*: 19. Rep. Guinea.
inspirata de Meillon & Wirth, 1981*c*: 592, South Africa.
lacustris Macfie, 1939*b*: 91. Uganda.
nigeriae Ingram & Macfie, 1923: 68 (*Ceratobezzia*). Nigeria; Gambia.
podagrica Goetghebuer, 1948: 17. Zaïre.
trimaculata Clastrier, 1983*a*: 24. Rep. Guinea.
usheri de Meillon, 1959*b*: 20. Mozambique.

Genus *Neurobezzia* Wirth & Ratanaworabhan

(Figs 306–307, 315)

Neurobezzia Wirth & Ratanaworabhan, 1972*b*: 244. Type species, *Bezzia granulosa* Wirth, by original designation.

Reference: Clastrier, 1983*c*: 64 (discussion).

Diagnosis: Small to medium size black midges; wing length 0,9–1,9 mm. Legs slender, unarmed; ♀ claws (Fig. 307) long and curved, equal on fore and mid legs, unequal on hind legs, those on fore and mid legs each with small, slender, inner basal tooth. Wing (Fig. 315) with costa long in ♀, extending nearly (*granulosa*, CR 0,92) or quite to wing tip (*tsacasi*); one broad radial cell; media forking at r–m crossvein. ♀ abdomen bicolored (*granulosa*) or entirely dark (*tsacasi*); two spermathecae. ♂ undescribed; the ♂ described by Grogan & Wirth (1978) was misidentified.

Immature stages and Biology: Unknown.

Distribution: Pacific Coast of North America, Seychelles; 2 species.

Afrotropical species:
tsacasi Clastrier, 1983*c*: 64. Seychelles.

Genus *Pellucidomyia* Macfie

(Figs 308, 317–319, 322)

Pellucidomyia Macfie, 1939*b*: 99. Type species, *Pellucidomyia ugandae* Macfie, by original designation.

Reference: Debenham, 1970*a*: 133 (diagnosis; figs.; immature stages; revision of Australasian species.).

Diagnosis: Body densely white or blackish pollinose above; head flattened anteroposteriorly, unflattened portion with same pollinosity as mesonotum. Eyes broadly separated, bare. Mesonotum conically produced forward, without or with only a small, blunt anterior tubercle. Legs (Figs 317–319) slender, femora unarmed, slightly clubbed distally; fore legs short, mid and hind legs longer; hind tarsus of ♀ extremely elongated. Fourth tarsomeres of fore and mid legs of ♀ cordiform, of hind leg cylindrical, very long and slender; fifth tarsomere unarmed, swollen on fore leg but not on mid and hind pairs. ♀ claws equal and simple or with minute basal tooth on fore and mid legs; single, long, and with or without minute basal tooth on hind leg. Wing (Fig. 308) with costa extending nearly to wing tip in ♀, shorter in ♂; one radial cell; r–m crossvein long, perpendicular to costa; no colour pattern. ♀ abdomen tapering distally, with pair of sparse setal tufts ventrally on eighth segment; two large, and sometimes one vestigial, spermathecae. ♂ genitalia with ninth tergum short and broad; aedeagus arched, expanded and setose medially; parameres broadly fused distally.

Immature stages: Larva unknown. Pupa (Fig. 322) with markedly elongated spinigerous tubercles segmentally arranged on abdomen; terminal processes stout, directed laterad at base, the tapering sharp apices bent caudad; prothoracic respiratory horn short, funnel-shaped, with spiracular openings arranged in a circle on truncated apex (Debenham, 1970*a*; 136, *P. leei* Debenham).

Biology: *Pellucidomyia sambulena* was reared from a pupa collected amongst debris in a small stream.

Distribution: Circumtropical; 8 species.

Afrotropical species:
sambulena de Meillon, 1942*a*: 14 (*Bezzia*). Mozambique.
ugandae Macfie, 1939*b*: 100. Uganda.

Genus *Tetrabezzia* Kieffer

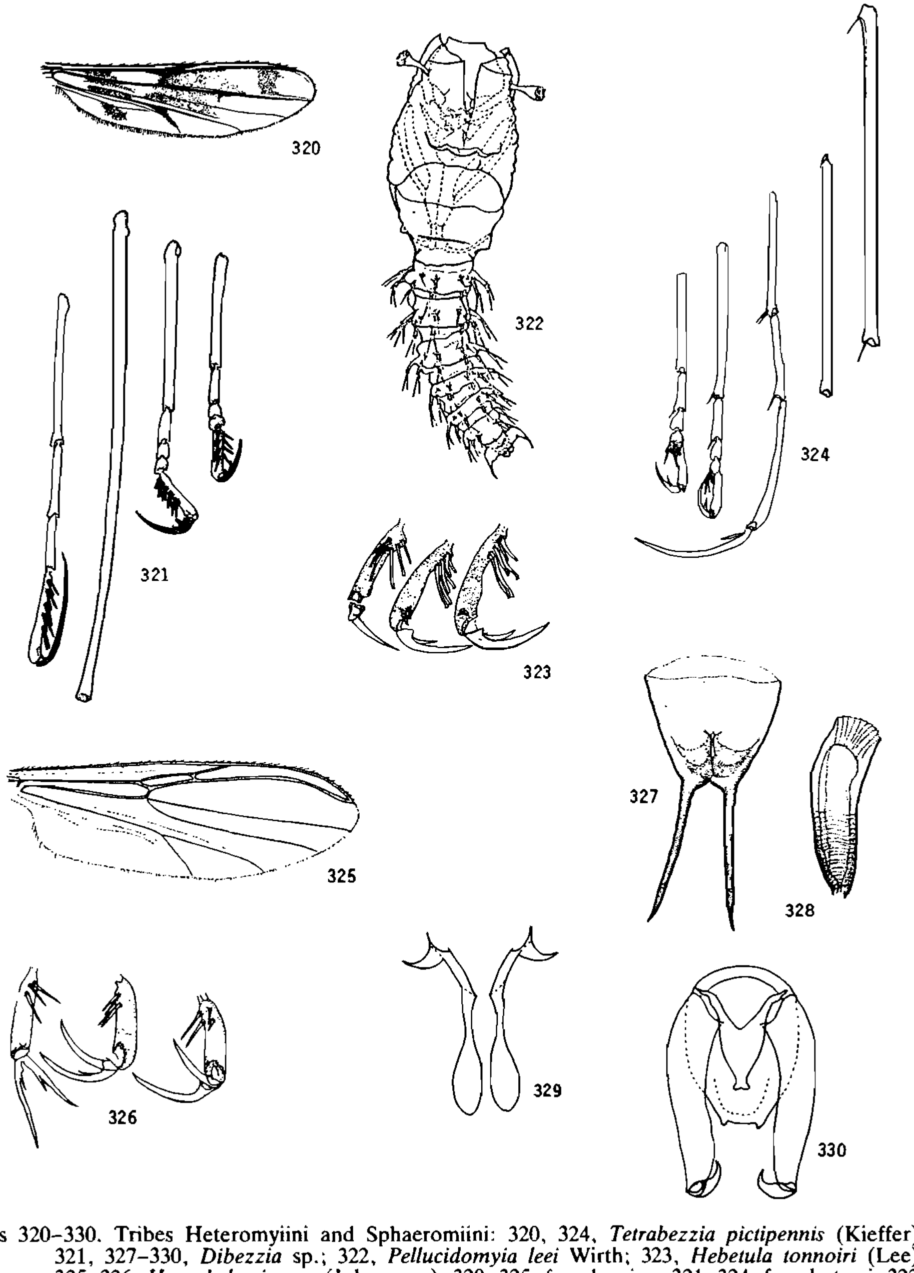
(Figs 320, 324)

Tetrabezzia Kieffer, 1917*b*: 296. Type species, *Dibezzia spinigera* Kieffer, by original designation.

Diagnosis: Large, slender, shining species with fasciate wing and silvery stripe across pleuron. Mesonotum with horizontally projecting anterior spine. Legs (Fig. 324) long and slender, especially hind pair; mid and hind femora unarmed, fore femur with a few small ventral spines distally; hind femur with distinct subapical dorsal swelling; hind tarsus of ♀ greatly elongated; fourth tarsomeres of fore and mid legs of ♀ with bifid spinose lobes, on hind leg long and simple; fifth tarsomeres without ventral armature, slender, extremely so on hind leg of ♀, not inflated on fore leg. ♀ claws much elongated with long inner basal tooth, especially long and slender on hind leg. Wing (Fig. 320) with costa long (CR 0,9); one radial cell. Abdomen long and petiolate, eighth segment without setal tufts; two spermathecae. ♂ genitalia with basistyle and dististyle long and slender; aedeagus subtriangular in outline without marked anterior arched concavity; parameres fused at bases, apices clavate.

Immature stages: Unknown.

Biology: *Tetrabezzia africana* was reared from roots and moss in shallow rock pools.



Figs 320–330. Tribes Heteromyiini and Sphaeromiini: 320, 324, *Tetrabezzia pictipennis* (Kieffer); 321, 327–330, *Dibezzia* sp.; 322, *Pellucidomyia leei* Wirth; 323, *Hebetula tonnoiri* (Lee); 325–326, *Homohelea insons* (Johannsen); 320, 325, female wing; 321, 324, female tarsi; 322, pupa; 323, 326, female fifth tarsomeres; 327, pupa, last segment; 328, pupal respiratory horn; 329, male parameres; 330, male genitalia, parameres omitted.

Distribution: Oriental and Afrotropical Regions; 6 species.

Afrotropical species:
africana Clastrier, 1982*b*: 307. Rep. Guinea; Nigeria.
argentea Ingram & Macfie, 1923: 70. Nigeria.
diazi de Meillon, 1961: 55. Madagascar.
soeiroi de Meillon, 1942*a*: 16 (*Bezzia*). Mozambique.

Tribe Sphaeromiini

Diagnosis: Large, nearly bare, predaceous midges (Figs 359, 374). ♀ antenna (Figs 344, 366) elongate; distal segments usually longer, cylindrical. Palpus (Figs 346, 362) 5-segmented, usually rather short; third segment without sensory pit. ♀ mandible (Fig. 365) with 7–12 strong teeth for insect feeding. Wing (Figs 325, 331, 339, 347, 354, 358) without macrotrichia; costa extending to more than 3/4 wing length, often shorter in ♂; media broadly sessile. ♀ tarsal claws large and straight (Fig. 333) to gently curved (Fig. 379). Tarsi with fifth tarsomere of ♀ armed ventrally with stout, blunt, black spines (batonnets) (Figs 333, 343, 350, 379). ♀ abdomen (Figs 336, 355, 363) without internal sclerotised gland rods and eversible glands. Two strongly sclerotised spermathecae (Figs 336, 349). ♂ genitalia (Figs 338, 342, 356, 369) variable, usually long and slender; basistyle simple, dististyle usually long and slender (fused to basistyle in *Nilobezzia*); aedeagus simple with low basal arch, distal process short; parameres separate, slender, distal blades usually clavate and markedly curved ventrad.

Immature stages: Larva long and slender, vermiform, swimming; lateral arms of epicranial suture usually obsolescent on anterior half of head. Pupa often with membranous glandular discs present on ventral side of several abdominal segments; these secrete an adhesive to attach the pupa to emergent vegetation, or other substrate.

Biology: Females are strongly predaceous on small soft-bodied insects, usually smaller than themselves, including males of their own species, which they capture from their mating swarms. The males thus serve as both mates and prey, and their genitalia are often found attached to the ♀ abdomen before oviposition, the remains of the male body having shrivelled and fallen away.

Genus *Dibezzia* Kieffer

(Figs 321, 327–330)

Dibezzia Kieffer, 1911*a*: 120. Type species, *Dibezzia clavata* Kieffer, by original designation.

Diagnosis: Large, slender, shining black species, wing length about 2 mm. Eyes contiguous, bare. Thorax with coarse, bent, setulae as in *Johannsenomyia*; mesonotum with a small, upright, anteromedian spine. Legs long and slender; femora armed or unarmed, slightly clubbed distally except hind pair distinctly clubbed. Tarsi (Fig. 321) slender, ♀ hind tarsus extremely elongate; fourth tarsomeres cylindrical; ♀ fifth tarsomeres armed ventrally with 4–5 pairs of batonnets along entire length of segment; ♀ claws unequal on all legs, each with short, blunt, external basal tooth. Wing relatively broad; two radial cells usually present, the crossvein between them sometimes more or less obsolete; costal ratio 0,8. ♀ abdomen petiolate, eighth segment without sclerotisation or ventral setal tufts; two large spermathecae. ♂ genitalia (Fig. 330) elongate, with greatly elongated, slender basistyle and short, hook-like dististyle; aedeagus simple, tapering; parameres (Fig. 329) separate, with straight, slightly expanded, paddle-shaped tips.

Immature stages: Larva unknown. Pupa with respiratory horn short, moderately broad (Fig. 328); abdomen with lateral posteromarginal tubercles developed as strong spines; last segment with greatly elongate, slender, pointed apical processes (Fig. 327).

Biology: *Dibezzia debenhamae* Wirth & Ratanaworabhan was reared from a pupa from a tree hole in Singapore.

Distribution: Oriental and Afrotropical Regions; 4 species.

Afrotropical species:
gideoni de Meillon & Wirth, 1981*c*: 595. South Africa.

Genus *Hebetula* Wirth & Debenham

(Figs 323, 358)

Hebetula Wirth & Debenham, 1977: 282. Type species, *Mixohelea lemur* Debenham, by original designation.

Diagnosis: Medium size, slender, shining midges; wing length 1,6–2,3 mm. Eyes bare, nearly contiguous. Mesonotum without anterior spine or tubercle. Legs slender to moderately stout; femora sometimes with stout ventral spines. Fourth tarsomeres cordiform; ♀ fifth tarsomeres (Fig. 323) armed ventrally at base with 2–3 pairs of batonnets, bare on distal half. ♀ tarsal claws (Fig. 323) simple, unequal on all legs (could be interpreted as a single long claw with slender basal tooth. Wing (Fig. 358) with two radial cells; costal ratio 0,8. ♀ abdomen with setal tufts of eighth segment inconspicuous. Two large spermathecae. ♂ genitalia short and broad; basistyle short and tapering; dististyle curved, moderately slender; aedeagus subtriangular, with low basal arch, apex simple; parameres fused at extreme base, slender distally with clavate tips.

Immature stages: Larva unknown. Pupa (after Debenham, 1974) with respiratory horn slender, apex not flared, spiracles restricted to apical part; anteromarginal tubercles each with a long seta; abdominal tubercles not prominent, apices squared; glandular discs absent; terminal processes of last segment short and stout.

Biology: Debenham (1974) reported two rearings of *Hebetula tonnoiri* (Lee) in Australia, from moss in a creek, and from a river margin.

Distribution: Australasian and Afrotropical Regions; 19 species.

Afrotropical species:
bequaerti Goetghebuer, 1933: 151. (*Palpomyia*). Zaïre.
hexacantha Kieffer, 1911*b*: 343 (*Sphaeromias*). Seychelles.

Genus *Homohelea* Kieffer

(Figs 325–326)

Homohelea Kieffer, 1917*b*: 364. Type species, *Palpomyia abjuncta* Kieffer, by designation of Macfie, 1940*a*: 26.

Schizodactylus Ingram & Macfie, 1921: 353. Type species, *Schizodactylus telmatoscopus* Ingram & Macfie (monobasic). Preoccupied by *Schizodactyla* Brulle.

Ankistrodactylus Ingram & Macfie, 1922: 272. Type species, *Schizodactylus telmatoscopus* Ingram & Macfie. New name for *Schizodactylus* Ingram & Macfie.

Reference: De Meillon & Wirth, 1981*b*: 542 (key to Afrotropical species).

Diagnosis: Moderately large, greyish pollinose, stout-bodied midges with whitish hyaline wings; wing length 2–3 mm. Eyes nearly contiguous, bare. Legs moderately stout, femora armed ventrally toward tip with 4–8 stout black spines; fourth tarsomeres cylindrical; fifth tarsomeres (Fig. 326) in ♀ armed with two pairs of batonnets near base; ♀ claws (Fig. 326) equal, long and curved, those on fore leg each with slender inner basal tooth. Wing (Fig. 325) with costa long, extending nearly to wing tip; two radial cells. ♀ abdomen without ventral setal tufts on eighth segment; two spermathecae. ♂ genitalia moderately short and stout; dististyle stout with slender hooked tip; aedeagus with high basal arch and stout, truncated, slightly flared tip; parameres fused except at base in a stout process with greatly expanded, rounded, pubescent distal lobe.

Immature stages: Larva unknown. Pupa dark brown, integument with numerous dark brown bosses; respiratory horn moderately long and slender, only slightly expanded distally and bearing a distal row of 12–14 spiracular openings; abdomen with prominent tubercles but no strong setae; caudal processes strong and divergent with spine-like tips.

Biology: *Homohelea albitudinis* was reared from a ground water pool, and *H. delanoe* was reared from a brackish, grassy marsh and from a stream margin.

Distribution: Australasian, Oriental and Afrotropical Regions; 13 species.

Afrotropical species:

albitudinis de Meillon & Wirth, 1981*b*: 543. South Africa.
delanoe de Meillon, 1942*b*: 113 (*Palpomyia*). Zimbabwe.
diabolis de Meillon, 1961: 52 (*Sphaeromias*). Madagascar.
longicosta Goetghebuer, 1933: 150 (*Palpomyia*). Zaïre.
melia de Meillon, 1943: 112. Zimbabwe; Gambia.
stuckenbergi de Meillon, 1961: 51 (*Sphaeromias*). Madagascar; Aldabra.
telmatoscopus Ingram & Macfie, 1921: 353 (*Schizodactylus*). Ghana.

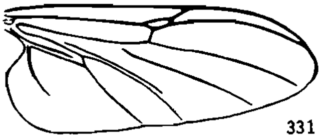
Genus *Jenkinshelea* Macfie

(Figs 331–338)

Jenkinsia Kieffer, 1913*a*: 165. Type species, *Jenkinsia setosipennis* Kieffer, by original designation. Preoccupied by *Jenkinsia* Jordan & Evermann.

Jenkinshelea Macfie, 1934: 177 (replacement name for *Jenkinsia* Kieffer).

Diagnosis: Moderately large, usually greyish pollinose species with ♀ wing unusually broad, anal angle greatly expanded; wing length 1,5–3,0 mm. Eyes broadly separated, bare. Mesonotum without anterior tubercle or spine, broadly rounded in front. Legs slender; femora unarmed ventrally; tarsomeres 3 and 4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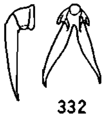
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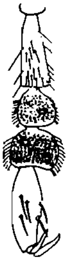
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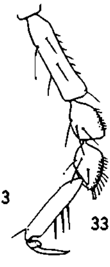
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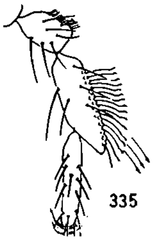
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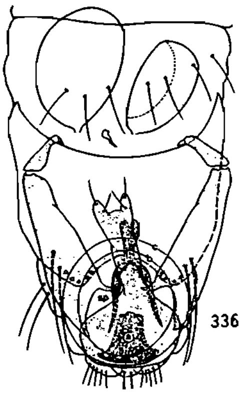

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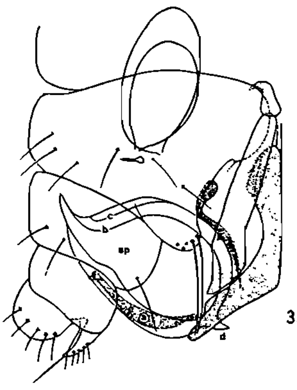

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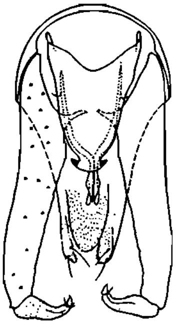
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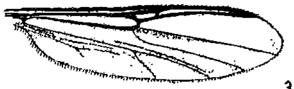
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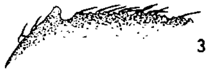
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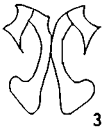
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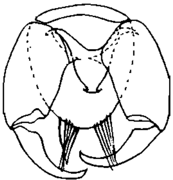
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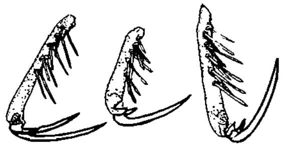
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Figs 331–343. Tribe Sphaeromiini: 331–338, *Jenkinshelea djalonensis* Clastrier; 339–343, *Johannsenomyia argentata* (Loew); 331, 339, female wing; 332, female claws, fore leg, side and end views; 333, female fore leg, tarsomeres 2–5; 334, female mid leg, tarsomeres 2–5; 335, female hind leg, tarsomeres 3–5; 336, 337, male and female genitalia, in copulo, ventral and lateral views; 338, male genitalia; 340, mesonotal tubercle and setulae; 341, male parameres; 342, male genitalia, parameres omitted; 343, female fifth tarsomeres.

with ventral pad of dense fine setae; tarsomere 4 cordiform, flattened ventrally; tarsomere 5 of ♀ armed ventrally with several batonnets (Figs 333–335). ♀ claws equal on all legs, bent at base, straight apically, each with short blunt external basal tooth (Fig. 332). Wing (Fig. 331) with r–m crossvein long, perpendicular; one or two radial cells; costa extending nearly to wing tip in ♀. ♀ abdomen (Figs 336–337) with deeply cleft eighth sternum with pair of dense long setal tufts; two large sac-like spermathecae. ♂ genitalia (Fig. 338) elongate; ninth tergum slender, tapering; basistyle and dististyle long and slender; aedeagus short, truncate basally with convex sides and rounded apex; parameres fused in midportion, forming a rounded basal arch, apices in form of slender, pointed, ventrally curved processes.

Immature stages: Larva with head long and slender, slightly tapered, without multiple setae; last abdominal segment about three times as long as broad; with four pairs of slender, moderately long, perianal setae. Pupa with short respiratory horn bearing 10–12 terminal spiracular openings; body with prominent blunt tubercles bearing small sharp spines; membranous glandular areas present on abdominal sterna; apical processes long and pointed, divergent.

Biology: *Jenkinshelea rhodesiensis* was reared from a stream margin and from among stalks of reeds in fairly fast flowing water on a river margin; *J. djalonensis* was reared from a rice field and a marsh; *J. polyxenae* was reared from a pond, and *J. trisensillata* was reared from dead leaves in a swamp.

Distribution: Nearctic, Oriental and Afrotropical Regions; 17 species.

Afrotropical species:
accraensis Ingram & Macfie, 1923: 41 (*Jenkinsia*). Ghana.
corea de Meillon, 1942*b*: 116. Zimbabwe.
djalonensis Clastrier, 1983*b*: 261. Rep. Guinea.
distincta de Meillon & Wirth, 1983*a*: 367. South Africa.
polyxenae de Meillon, 1936: 189. South Africa.
rhodesiensis de Meillon, 1937: 261. Zimbabwe; Mozambique, Ivory Coast.
sudwalai de Meillon & Wirth, 1983*a*: 369. South Africa.
trisensillata Clastrier, 1983*b*: 266. Rep. Guinea.

Genus *Johannsenomyia* Malloch

(Figs 339–343)

Johannsenomyia Malloch, 1915: 332. Type species, *Johannsenomyia halteralis* Malloch (= *Ceratopogon argentatus* (Loew), by designation of Wirth, 1952*a*: 211.

Dicrohelea Kieffer, 1917*b*: 363. Type species, *Palpomyia filicornis* Kieffer, by designation of Macfie, 1940*a*: 26.

Diagnosis: Slender, usually shining species; wing length 2–3 mm. Eyes bare, contiguous. Mesonotum (Fig. 340) with small, upright, anteromedian tubercle; surface of integument with short appressed setulae arising from microtubercles. Legs long and slender, femora somewhat clubbed, especially on hind legs; femora usually unarmed. Fourth tarsomeres cylindrical, at least on hind leg; fifth tarsomeres (Fig. 343) of ♀ armed ventrally with numerous batonnets; fifth tarsomere of ♂ hind leg armed with 2–3 pairs of batonnets. Claws of ♀ equal on fore legs, very unequal on mid and hind legs, the longer claw only slightly curved, each claw with short, stout, external basal tooth (Fig. 343). Wing (Fig. 339) with two radial cells (rarely one); costa moderately long, costal ratio about 0,8. ♀ abdomen more or less petiolate, narrowed at base, eighth segment without ventral setal tufts; two large spermathecae. ♂ genitalia (Fig. 342) rotated and appressed obliquely against apex of abdomen with sternal side facing caudad; ninth tergum rounded distally; aedeagus broad, with well-developed basal arch and broad, cap-like tip; parameres (Fig. 341) separate, distal portions approximate, basal portion of each slender and curved, distal portion expanded into a broad, platelike, laterally flattened tip.

Immature stages: Larva undescribed. Pupa with respiratory horn 3–4 times as long as breadth of flaring portion; abdominal tubercles inconspicuous, not conical or angulate; abdominal sterna without glandular discs. The eggs are deposited in spiral bands 30–40 mm in length while the ♀ hovers several cm above the water surface in sheltered places.

Biology: *Johannsenomyia albidorsata* was reared from a river margin (Mayer 1957).

Distribution: Worldwide except Palaearctic; 26 species.

Afrotropical species:

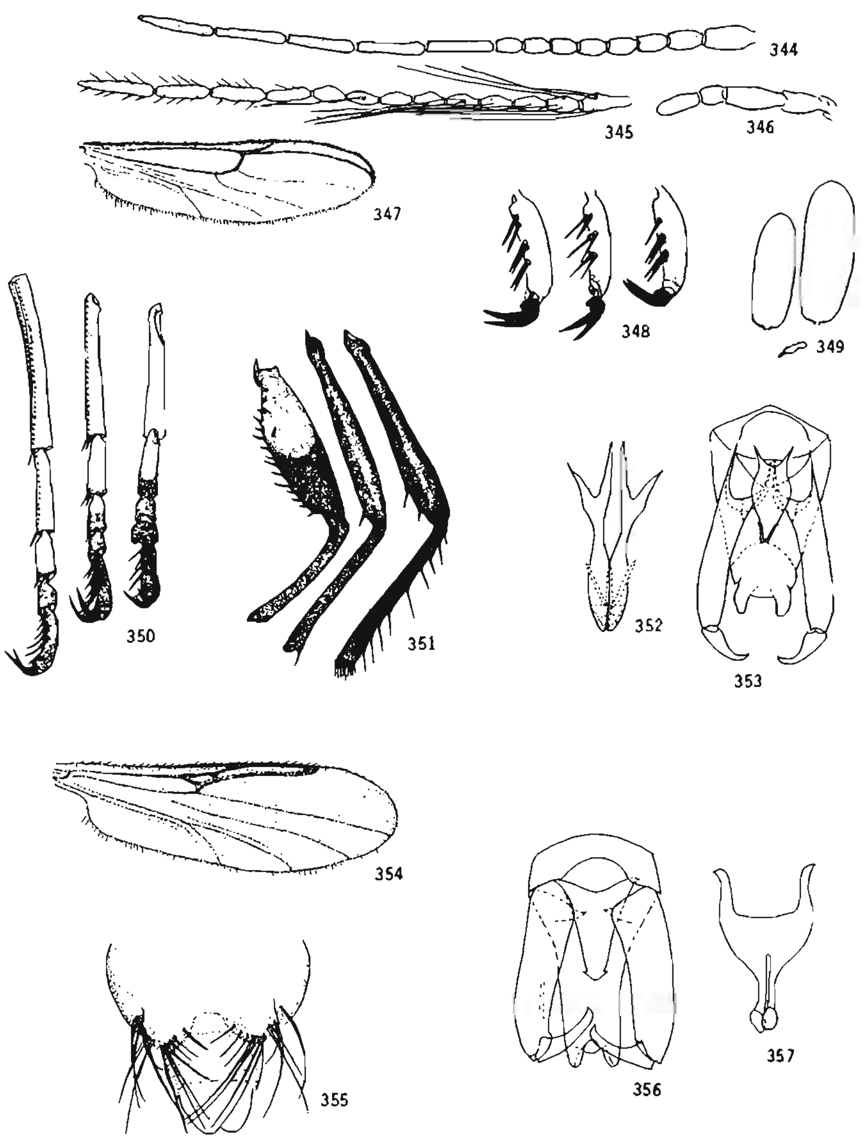
albidorsata de Meillon, 1937: 368 (*Dicrohelea*). South Africa; Madagascar, Zimbabwe.
angulosa de Meillon & Wirth, 1983*a*: 369. South Africa. Zimbabwe.
grahami Ingram & Macfie, 1923: 65 (*Palpomyia*). Nigeria.
nigeriae Ingram & Macfie, 1923: 65 (*Palpomyia*). Nigeria.
nigra Goetghebuer, 1933: 149. Zaïre.
schoutedeni Goetghebuer, 1933: 150 (*Palpomyia*). Zaïre.

Genus *Mackerrasomyia* Debenham

(Figs 350–351)

Mackerrasomyia Debenham, 1970*b*: 140. Type species, *Heteromyia brevibarba* Kieffer, by original designation.

Diagnosis: Moderately large species, wing length 2,2–2,4 mm. Eyes bare, widely separated. Mesonotum with strong anterior tubercle. Legs (Fig. 351) with fore femur greatly swollen, with numerous short, stout, ventral spines; hind femur weakly clubbed distally, mid and hind femora with 1–2 ventral preapical spines; fore tibia strongly arcuate, with blunt apical projection. Fourth tarsomeres cordiform; fifth tarsomeres armed with several pairs of batonnets, the distal one or two pairs separated from the others (Fig. 350). ♀ claws paired and equal on all legs; each with a short inner basal tooth (Fig. 350). Wing narrow; costal ratio 0,75; two radial cells, second about twice as long as first. ♀ abdomen with one spermatheca. ♂ genitalia with expanded, bowl-like ninth tergum; basistyles swollen and arcuate, their bases joined behind aedeagus; dististyle long and broad, nearly straight; aedeagus a small plate-like structure with short basal arms and broad,



Figs 344–357. Tribe Sphaeromiini: 344–349, 352–353, *Macropeza natalensis* (de Meillon); 350–351, *Mackerrasomyia brevibarbis* (Kieffer); 354–357, *Mallochohelea albibasis* (Malloch); 344, female antenna; 345, male antenna; 346, female palpus; 347, 354, female wing; 348, female fifth tarsomeres; 349, spermathecae; 350, female tarsi; 351, female femora and tibiae; 352, 357, male parameres; 353, 356, male genitalia, parameres omitted; 355, female genitalia.

cap-like tip. Parameres separate, each a stout curving sclerite with expanded tip and wing-like basal apodeme.

Immature stages and Biology: Unknown.

Distribution: Old World Tropics; 6 species.

Afrotropical species:
zumpti de Meillon & Wirth, 1979*a*: 182. Zimbabwe.

Genus *Macropeza* Meigen
(Figs 344–349, 352–353, 359)

Macropeza Meigen, 1818: 87. Type species, *Macropeza albitarsis* Meigen, by original designation.
Macroptilum Becker, 1903: 76. Type species, *Macroptilum nudum* Becker, by monotypy.

References: Macfie, 1939*a*: 1 (revision; key); Wirth & Ratanaworabhan, 1972*a*: 213 (diagnosis; species list).

Diagnosis: Large slender species with narrow wings (Fig. 359); wing length 4–6 mm. Eyes separated, bare. Antenna (Fig. 344) slender, in ♂ (Fig. 345) with sparse plume. Palpus as in Fig. 346. Mesonotum convex, sometimes somewhat produced conically over head, without anterior spine or tubercle. Legs slender, elongate; femora unarmed ventrally, not thickened distally; fourth tarsomeres cordiform; fifth tarsomeres of ♀ (Fig. 348) armed ventrally with several batonnets. ♀ claws (Fig. 348) short and curved, stout at base, pointed apically; equal on all legs, each with a short, blunt, outer basal tooth. ♀ wing (Fig. 347) long and narrow, anal angle usually well developed, often rectangular; one radial cell; costa usually reaching apex of wing, radial cell usually at least moderately broad; r–m crossvein elongate, often perpendicular to costa, usually located near mid-length of wing, sometimes distinctly distad. ♂ with radial cell much shorter, not reaching wing tip. ♀ abdomen with pair of conspicuous lateral setal tufts on eighth sternum, often with ventral sclerotisation near gonopore; two large spermathecae (Fig. 349). ♂ genitalia (Fig. 353) long and slender, basistyle elongate, dististyle short; aedeagus short with broad base and blunt tip; parameres (Fig. 352) separate, each with strongly sclerotised, ventrally recurved, hook-like process.

Immature stages: Larva (of *M. natalensis*) rather stout, with slender, anteriorly tapering head; body without visible setae. Pupa with respiratory horn short, with bluntly rounded tip bearing 14–20 spiracular openings; abdominal segments with short, semi-erect spines; apical processes moderately long and pointed, slightly divergent.

Biology: The larval habitats are known for five Afrotropical species: a river margin, the margin of a water storage dam, a water storage reservoir, a stream margin, from a borrow pit with scanty vegetation, and from plants of the water lettuce, *Pistia stratiotes* L.

Distribution: Holarctic, Oriental and Afrotropical Regions; 23 species.

Afrotropical species: The Afrotropical Catalogue lists 16 species; additions and corrections:
geari de Meillon & Wirth, 1981*b*: 547. South Africa.

Genus *Mallochohelea* Wirth

(Figs 354–357)

Mallochohelea Wirth, 1962: 278. Type species, *Johannsenomyia albibasis* Malloch, by original designation.

Reference: De Meillon & Wirth, 1981*b*: 552 (key to Afrotropical species).

Diagnosis: Slender to moderately stout midges, integument usually shining; wing length 2–3 mm. Eyes moderately separated, bare. Legs slender to moderately stout, hind femur not markedly clubbed; femora with or without ventral armature; fourth tarsomeres cylindrical; fifth tarsomeres of ♀ with 5–8 pairs of batonnets covering the length of segment. ♀ claws long, equal, bent at base, nearly straight distally, each claw with short external basal tooth. Wing (Fig. 354) with two radial cells (rarely one); costal ratio about 0,8. ♀ abdomen with pair of ventral setal tufts on eighth segment (Fig. 355); two large spermathecae. ♂ genitalia (Fig. 356) with long basistyle and dististyle; aedeagus with low basal arch, tapered distally to moderately broad cap-like tip; parameres (Fig. 357) fused in midportion forming a rounded basal arch, extending distad as a pair of contiguous, slender, dorsally curved rods with ends slightly capitate.

Immature stages: Larva (after Glukhova, 1978) with head moderately broad and tapering, only the *o* and *u* setae multiple; epipharynx with one pair of combs, and a toothed comb on the lateral arm. Pupa with respiratory horn very short, 1,5–2,0 times as long as broad; abdominal segments with prominent, angular, backward projecting, spinose tubercles; abdominal sterna 6 and 7 with membranous glandular discs; caudal processes relatively short and pointed.

Biology: *Mallochohelea errinae* (de Meillon) was reared from a river margin, and *M. fluminea* was reared from a stream margin and the margin of a water storage dam.

Distribution: Worldwide; 49 species.

Afrotropical species: The Afrotropical Catalogue lists 6 species; additions and corrections:

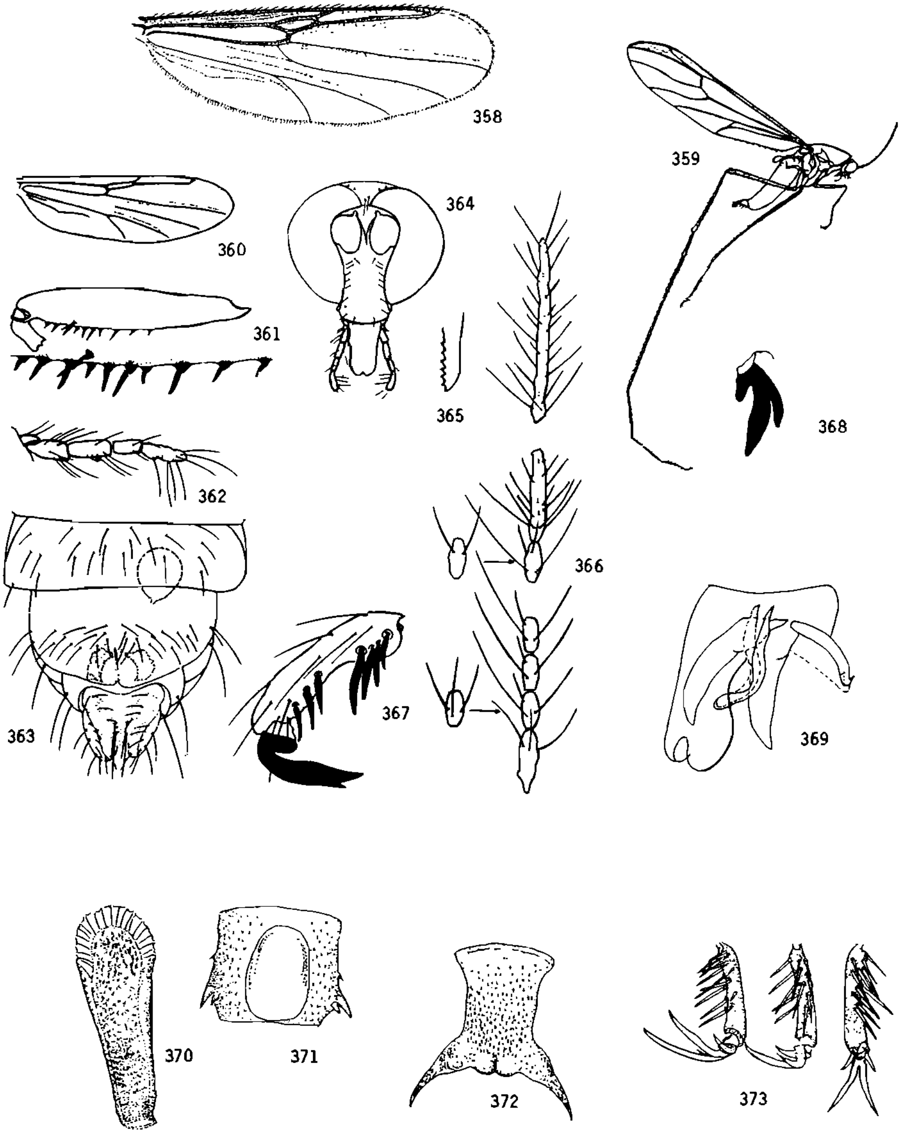
aukurabis de Meillon & Wirth, 1983*a*: 371. South Africa.
fluminea de Meillon & Wirth, 1981*b*: 550. South Africa.
hamata de Meillon & Wirth, 1987*a*: 60. Madagascar.
hansfordi de Meillon & Wirth, 1983*a*: 372. South Africa.
santaeluciae de Meillon, 1937: 365 (*Palpomyia*). South Africa. New combination.
unca de Meillon & Wirth, 1987*a*: 61. Kenya

Genus *Neosphaeromias* Das Gupta & Wirth

(Figs 360–368)

Neosphaeromias Das Gupta & Wirth, 1971: 875. Type species, *Neosphaeromias gibbus* Das Gupta & Wirth, by original designation.

Diagnosis: Medium size to large, stout-bodied species; wing length 2,8–3,0 mm. Eyes moderately separated, bare (Fig. 364). Antenna as in Fig. 366; palpus as in Fig. 362; mandible as in Fig. 365. Mesonotum with strong erect anteromedian



Figs 358–373. Tribe Sphaeromiini: 358, *Hebetula tonnoiri* (Lee); 359, *Macropeza longipes* (Séguy); 360–368, *Neosphaeromias afrotropicalis* Clastrier; 369–373, *Nilobezzia schwarzii* (Coquillett); 358, 360, female wing; 359, female habitus; 361, female fore femur; 362, female palpus; 363, female genitalia; 364, female head; 365, female mandible; 366, female antenna (partial); 367, female hind leg, tarsomere 5; 368, female fore leg, claw; 369, male genitalia, side view; 370, pupal respiratory horn; 371, pupal abdomen, glandular disc; 372, pupa, last abdominal segment; 373, female fifth tarsomeres.

spine. Fore femur (Fig. 361) greatly swollen, with 10–30 stout ventral spines, mid and hind femora slender, unarmed; fore tibia arcuate; fourth tarsomeres cordiform; fifth tarsomeres (Fig. 367) of ♀ each with 12–16 batonnets along entire length. ♀ claws equal on all legs, bent at base, straight and flattened distally; each (Fig. 368) with small external basal tooth and a longer, pointed, internal basal tooth. Wing (Fig. 360) with two radial cells; costa relatively short, costal ratio 0,7–0,8. ♀ abdomen (Fig. 363) without ventral setal tufts or sclerotisation on segment eight; one spermatheca. ♂ genitalia short and stout; basistyle short with well-developed mediangular process; dististyle rather stout, short to long; aedeagus broad, tapering to bluntly rounded tip; parameres separate, slender to stout in midportion, with lamellate or abruptly bent, hooked tip. Immature stages unknown.

Biology: *N. afrotropicalis* was reared from mud in a rice field, from a pond margin, and from vegetation in a pool with rapid current.

Distribution: Australasian, Oriental and Afrotropical Regions; 4 species.

Afrotropical species:
afrotropicalis Clastrier, 1983*b*: 268. Rep. Guinea.

Genus *Nilobezzia* Kieffer

(Figs 369–373)

Nilobezzia Kieffer, 1921*b*: 24. Type species, *Nilobezzia armata* Kieffer, by monotypy.

Diagnosis: Robust, usually large, dull or pollinose species; wing length 2–4 mm. Eyes bare, nearly contiguous. Antenna often rather short, with inconspicuous verticils; ♂ with inconspicuous plume. Legs slender, femora moderately stout; femora with ventral and tibiae with dorsal, widely spaced bristles or slender spines; fourth tarsomeres not cordiform; ♀ fifth tarsomeres (Fig. 373) armed ventrally with numerous batonnets. ♀ claws (Fig. 373) large, equal, bent at base and nearly straight distally; each with short, stout, external basal tooth. Wing with one or two radial cells; costa moderately short, costal ratio 0,8; wing often whitish at base with distal or marginal infuscation. ♀ abdomen with sclerotisation and pair of setal tufts on eighth sternum; two spermathecae. ♂ genitalia (Fig. 369) rotated and bent ventrad so that sternal surface is oriented caudad, with very poorly developed basistyle and dististyle, the latter thumb-like and not movable. Aedeagus with short basal arch and cap-like apex; parameres fused in an H-shaped structure, basal arms not markedly divergent, the slender distal lobes contiguous mesad and abruptly curved or bent dorsad distally.

Immature stages: Larva (after Debenham 1974) nearly bare, all segments broader than head; head conical, 1,5 times as long as broad; mandible large, stout and strongly curved; anal segment with long setae. Pupa with respiratory horn (Fig. 370) short, about three times as long as distal breadth, slightly flared distally; abdominal tubercles prominent, stout and rounded, or conical and pointed, but not bent and directed caudad; glandular discs (Fig. 371) present on abdominal sterna 5–7 in some species, absent in others; caudal processes (Fig. 372) short and conical, strongly divergent, with black spine-like tip. The immature stages of *Nilobezzia robusta* (de Meillon) were described by Mayer (1955).

Biology: *Nilobezzia belligera* (de Meillon) was reared from a pupa in sparse vegetation at the edge of a small lake with very clear deep water, and from a river margin; *N. nigritibialis* (Ingram & Macfie) was reared from a pupa in algae in a water reservoir; and *N. robusta* (de Meillon) was reared from a rainwater pool and from sand in shallow water of the Berg River.

Distribution: Worldwide; 64 species.

Afrotropical species: The Afrotropical Catalogue lists 8 species; additions and corrections: None.

Genus *Sphaeromias* Curtis

(Figs 374–379)

Sphaeromias Curtis, 1829: 285. Type species, *Sphaeromias albomarginatus* Curtis, by original designation.

Reference: De Meillon & Wirth, 1987*a*: 64 (key to Afrotropical species).

Diagnosis: Large, stout, grayish pollinose midges (Fig. 374); wing length 3–5 mm. Eyes bare, nearly contiguous. Mesonotum with small, pointed, anterior tubercle. Legs slender; femora with ventral and tibiae with numerous strong dorsal setae or small sharp spines (Fig. 378); fourth tarsomeres cylindrical; ♀ fifth tarsomeres (Fig. 379) armed ventrally with numerous batonnets the length of segment. ♀ claws (Fig. 379) large, equal, curved, each with slender, sharp-pointed, inner basal tooth. Wing (Fig. 375) with two radial cells; costa long, extending nearly to wing tip. ♀ abdomen without sclerotisation or setal tufts on eighth segment; two spermathecae. ♂ genitalia (Fig. 377) with long basistyles and dististyles; aedeagus with well-developed basal arch and broad, cap-like tip; parameres (Fig. 376) joined in a V-shaped notch at base, fused distally in a long, tongue-like lobe.

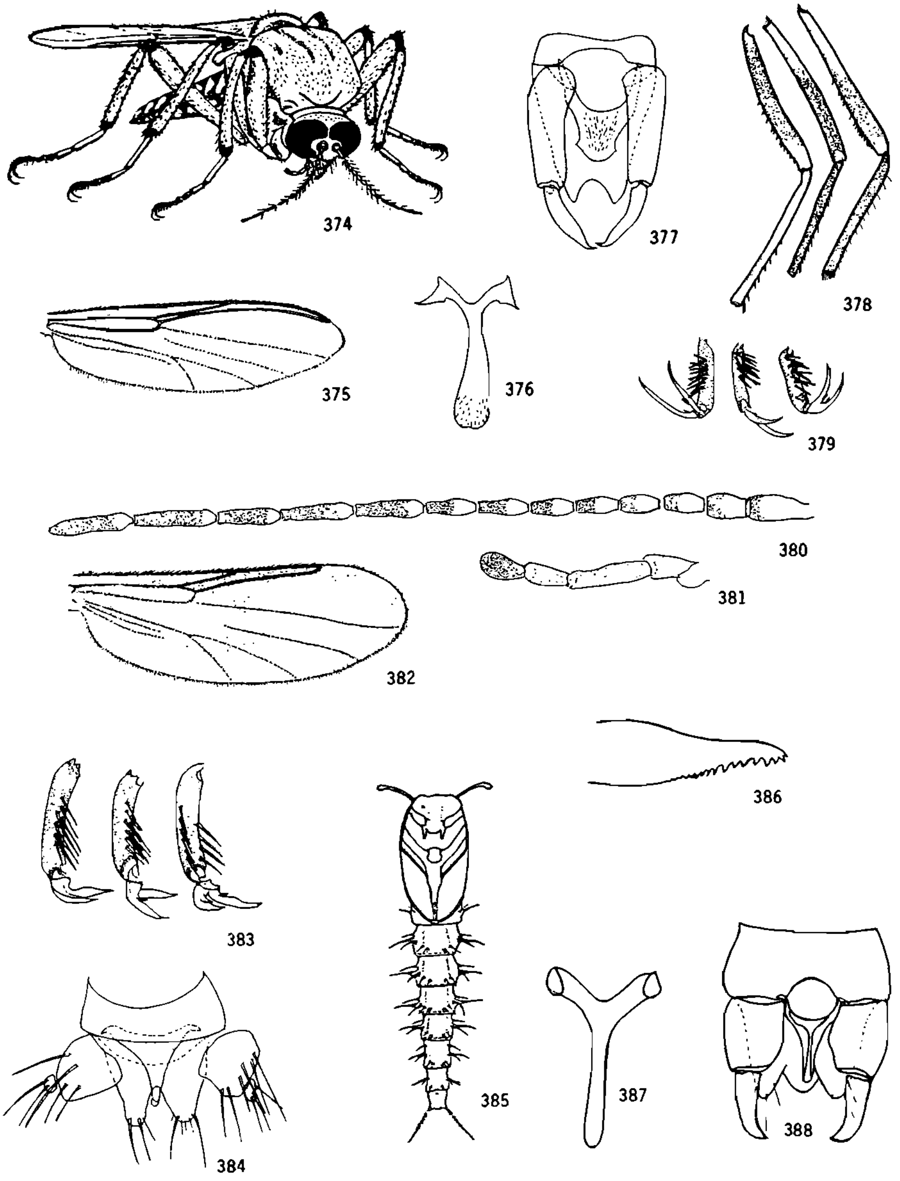
Immature stages: Larva with head rather short and ovoid, slightly tapering, twice as long as broad; eye kidney-shaped, located far caudad on head; *o*, *s*, and *u* setae multiple; last segment with four pairs of short, slender, lateral setae, and two minute pairs of perianal setae. Pupa with respiratory horn elongate, tapering from broad rounded apex; abdominal tubercles prominent, conical and sharp-pointed; abdomen without ventral glandular discs; caudal processes moderately long, tapering, divergent.

Biology: Larval habitats have been recorded for five Afrotropical species: from plants of the water hyacinth, *Pistia stratiotes* L., from peat soil under *Rhizophora* mangroves, from a grassy 'vlei', and from a shady swamp.

Distribution: Worldwide; 37 species.

Afrotropical species:

corsoni Ingram & Macfie, 1924*c*: 182 (*Ankistrodactylus*). Ghana.
eugenei de Meillon & Wirth, 1987*a*: 62. Zimbabwe.
litoraureus Ingram & Macfie, 1921: 359. Ghana.
meeseri de Meillon, 1942*b*: 95. Zimbabwe.



Figs 374–388. Tribes Sphaeromiini and Palpomyiini: 374, *Sphaeromias fasciatus* (Meigen); 375–379, *Sphaeromias longipennis* (Loew); 380–382, 386–388,, *Bezzia setulosa* (Loew); 383–384, *Phaenobezzia pistiae* (Ingram & Macfie); 385, *Bezzia glabra* (Coquillett); 374, female habitus; 375, 382, female wing; 376, 387, male parameres; 377, 384, 388, male genitalia, parameres omitted; 378, female femora and tibiae; 379, 383, female fifth tarsomeres; 380, female antenna; 381, female palpus; 385, pupa; 386, female mandible.

par Ingram & Macfie, 1922: 272 (*Ankistrodactylus*). Ghana; Gambia, Madagascar.
pistiae Ingram & Macfie, 1922: 272 (*Palpomyia*). Ghana.
servilia de Meillon, 1942*a*: 25. Mozambique.
theileri de Meillon & Wirth, 1981*b*: 552. South Africa.

Genus *Xenohelea* Kieffer

Xenohelea Kieffer, 1917*b*: 295. Type species, *Xenohelea pruinosa* Kieffer, by original designation.

Diagnosis: ♀ (male undescribed): Moderately large (wing length 2–3 mm) slender midges, thorax with whitish or grayish pollen. Eyes contiguous, bare. Mesonotum with setae arising from distinct tubercles forming dark punctations. Legs slender, fore femur slightly arcuate; femora armed ventrally with numerous stout spines; fourth tarsomeres short, cylindrical; ♀ fifth tarsomeres armed ventrally with usually 4–6 pairs of batonnets along entire length of segment. ♀ claws unequal, simple on all legs (could be interpreted as a single long claw with slender basal tooth. Wing slender; two radial cells (rarely one); costal ratio 0,8. Abdomen slender; eighth segment without sclerotisation or ventral setal tufts; two large spermathecae.

Immature stages: Larva unknown. Pupa with respiratory horn five times as long as broad, with nine apical spiracular openings.

Biology: *Xenohelea galatea* was reared from a pupa collected among debris in a small clear stream (Mayer 1957).

Distribution: Oriental and Afrotropical Regions; 12 species.

Afrotropical species:
galatea de Meillon, 1942*a*: 23. Mozambique; Madagascar.
spinosipes Goetghebuer, 1948: 13 (*Palpomyia*). Zaïre.

Tribe Palpomyiini

Diagnosis: Large (wing length 2–3 mm), nearly bare, predaceous midges. Body not unusually slender or dorsoventrally flattened. ♀ antenna (Fig. 380) short to elongate, distal five segments usually longer, cylindrical, verticils sparse. Palpus (Fig. 381) 5-segmented, usually short and slender; third segment with sensilla not borne in a sensory pit. ♀ mandible (Fig. 386) with 10–20 coarse teeth, and with finer proximal teeth in series. Thorax robust, mesonotum usually with anterior spine or tubercle. Legs not extremely long or setaceous; femora often armed, fore femur sometimes swollen; fourth tarsomeres more or less cordiform; fifth tarsomeres (Figs 383, 398) not armed ventrally or with only sharp-tipped spines; ♀ claws equal, usually moderately long, usually with small inner basal tooth. Wing (Figs 382, 397) without macrotrichia; costa extending to more than 3/4 wing length; one or two radial cells; media usually broadly sessile. ♀ abdomen with internal sclerotised gland rods and eversible glands from terga; eighth sternum (Fig. 400) without prominent setal tufts; one or two spermathecae. ♂ genitalia variable; tergum usually short with prominent cerci (Fig. 399).

Immature stages: Larvae vermiform, long and slender; anterior and posterior pseudopods absent; last segment with rather long, more or less anteriorly directed perianal setae; head capsule well developed; mouthparts reduced; pharyngeal skeleton with three combs, the principal comb divided. Pupa (Fig. 385) stout anteriorly, abdomen tapered distally; prothoracic respiratory horn rather elongate, expanded distally with row of terminal spiracular openings; abdominal segments 3–7 similarly bristled; last segment with a bristle-bearing tubercle.

Biology: Females are predaceous, preying on small soft-bodied insects.
Larvae are usually aquatic.

Genus *Bezzia* Kieffer
(Figs 380–382, 385–388)

Bezzia Kieffer, 1899: 69. Type species, *Ceratopogon ornatus* Meigen, by original designation.

References: Haeselbarth, 1965*a*: 1 (revision *nicator* Group); Haeselbarth, 1975: 352 (revision *africana* Group); Remm, 1974: 429 (diagnosis; subgenera; revision of species of the U.S.S.R.; Wirth & Grogan, 1983: 489 (generic diagnosis).

Note: Remm (1974) used several well-founded subgenera for the Palaearctic species of *Bezzia*, and Wirth & Grogan (1983) applied these to the North American species. The use of subgenera for the Afrotropical Region must await a comprehensive revisionary study of the African species.

Diagnosis: Small to large, stocky, nearly bare, predaceous midges; wing length 1–4 mm. Thorax robust, mesonotum usually with anterior spine or tubercle, with several strong supra-alar and postalar setae. ♀ mandible as in Fig. 386. Wing (Fig. 382) with one radial cell; costal ratio 0,6–1,0; vein M2 originating near r–m crossvein but may slightly more distad or proximad; macrotrichia absent. Legs slender, sometimes with numerous spine-like setae; fore femur with 0–10 stout ventral spines; fourth tarsomeres short and more or less cordiform; fifth tarsomeres of ♀ without ventral batonnets or strong, sharp-pointed setae. ♀ claws simple and equal, usually with small inner basal tooth. ♀ abdomen with 1–5 pairs of sclerotised gland rods; two spermathecae. ♂ genitalia (Fig. 388) inverted; ninth tergum short with prominent setose cerci, without sclerotised apicolateral processes; aedeagus variably shaped, usually triangular in outline, often with ventral surface spiculate; parameres (Fig. 387) fused to form an unpaired distal process, usually rod-like but sometimes variable in shape; dististyle well developed and articulated, setose.

Immature stages: Larva with head long and slender, usually subcylindrical and very little tapering; perianal setae usually elongate. Pupa (Fig. 385) usually with respiratory horn elongate and expanded toward tip which bears 13–60 spiracular openings; operculum with 2–4 setae.

Biology: Larval habitats have been recorded for 11 Afrotropical species: rice fields, river and other stream margins, seepage pools, margin of a brackish spring; hoofprints in a sandy creek bed; margin of a water storage dam, and from moss on a wall.

Distribution: Worldwide; 262 species.

Afrotropical species: The Afrotropical Catalogue lists 32 species; additions and corrections:

amana de Meillon & Wirth, 1981*b*: 554. South Africa.
dessarti Haeselbarth, 1980: 656. Zaïre.
haroldi de Meillon & Wirth, 1987*a*: 66. South Africa.
insolita de Meillon & Wirth, 1983*a*: 376. South Africa.
lophophora Clastrier, 1988*b*: 58. Rep. Guinea.
spinosella Clastrier, 1983*c*: 376. Seychelles.
turrita de Meillon & Wirth, 1983*a*: 378. South Africa.

Genus *Palpomyia* Meigen

(Figs 397–400)

Palpomyia Meigen, 1818: 82. Type species, *Ceratopogon flavipes* Meigen, by monotypy.

References: Goetghebuer, 1948: 16 (key to Zaïre species); de Meillon & Wirth, 1987*a*: 71 (partial key).

Diagnosis: Small to large, slender to moderately robust midges, body nearly bare; wing length 1–5 mm; ♂ usually much smaller than ♀. Eyes bare, usually well separated. Thorax robust; mesonotum with uniform fine pubescence and usually with small anterior spine or tubercle. Legs slender; fore femur slender to greatly swollen, usually with stout ventral spines; mid and hind femora slender and often with ventral spines; fourth tarsomeres (Fig. 398) cordiform or bilobed; fifth tarsomeres unarmed or with two ventrolateral rows of stout bristle-like setae; ♀ claws (Fig. 398) moderately small to enlarged, with or without small inner basal tooth. Wing (Fig. 397) narrow to moderately wide; hyaline to infuscated; two radial cells; costa usually extending 2/3 wing length or more, but not to tip. ♀ abdomen (Fig. 400) usually with paired eversible glands and internal sclerotised gland rods (as in *Stenoxenus*, Fig. 401); two, occasionally three, spermathecae; eighth sternum usually large and cleft posteriorly; ninth sternum with arms usually anteriorly directed. ♂ genitalia (Fig. 399) with prominent cerci on ninth tergum; basistyle simple or with setose mesoventral tubercle or lobe; dististyle articulated; aedeagus more or less conical or triangular, ventral surface usually spiculate; parameres fused or divided, usually with well-developed basal apodeme.

Immature stages: Larva slender and vermiform; head 2–4 times longer than broad, but usually not so elongate or cylindrical as in *Bezzia*; last segment with one pair of short setae and four pairs of longer perianal setae. Pupa with 2–4 pairs of *am* tubercles on operculum, posterior most pair always bearing a single long seta; respiratory horn slender, tip usually broader than base, without scales or other ornamentation, apex with a single row of up to 40 spiracular openings; abdominal segments usually covered with fine-pointed or rounded tubercles, 2–5 *dpm*, 3 *lpm*, 1–2 *dasm*, 2–3 *vpm*, 0–1 *lasm* tubercles; caudal processes of last segment usually lacking spicules.

Biology: Larvae usually do not swim so vigorously as in *Bezzia* or the Sphaeromiini. *Palpomyia fusca* de Meillon was reared from a swamp with dense vegetation, *P. magali* de Meillon and *P. singularis* de Meillon from river margins, and *P. nigrithorax* de Meillon from pupae collected in an exposed pool.

Distribution: Worldwide; 248 species.

Afrotropical species: The Afrotropical Catalogue lists 22 species; additions and corrections:

armigera de Meillon & Downes, 1986: 177. South Africa.
gilva de Meillon & Wirth, 1987*a*: 67. South Africa.
kurwana de Meillon & Wirth, 1987*a*: 69. South Africa.
magali de Meillon & Wirth, 1981*b*: 557. South Africa.
verna de Meillon & Wirth, 1987*a*: 70. South Africa.

Genus *Phaenobezzia* Haeselbarth

(Figs 383–384)

Phaenobezzia Haeselbarth, 1965*b*: 297. Type species, *Probezzia pistiae* Ingram & Macfie, by original designation.

References: Haeselbarth, 1965*b*: 297 (revision and key); Grogan & Cornet, 1985: 678 (synonymy).

Diagnosis: Moderately large, slender, nearly bare midges; wing length 2–3 mm. Eyes bare, narrowly to broadly separated. Mesonotum with or without anterior tubercle. Legs slender, femora unarmed; fourth tarsomeres slightly cordiform; ♀ fifth tarsomeres (Fig. 383) armed ventrally with more or less strong, sharp, spine-like setae with bent tips; ♀ claws (Fig. 383) evenly curved or bent at base, equal, each with small inner basal tooth. Wing with coarse microtrichia, macrotrichia absent; one radial cell (except in *cinnae*); costa long, extending to 0,82–0,87 of wing length. ♀ abdomen with 1–5 pairs of dorsal gland rods and eversible glands; two large spermathecae. ♂ genitalia (Fig. 384) with short ninth tergum; basistyle short and bulbous, dististyle absent or very small and imperfectly articulated; aedeagus triangular, ventral membrane spiculate; parameres fused, rodlike, with butterfly-shaped bases.

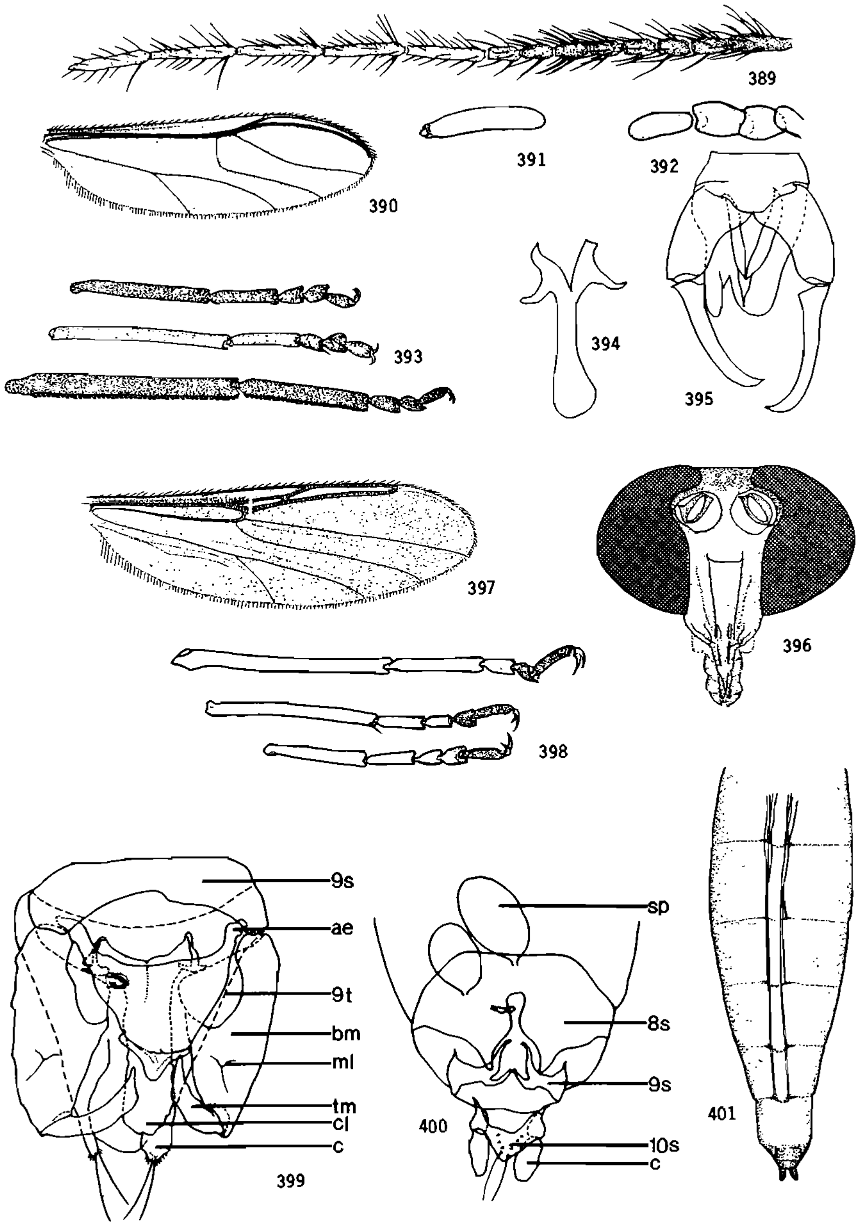
Immature stages: Larva (after Ingram & Macfie, 1921; *pistiae*) with head yellow, about four times as long as broad; body eel-like and slender, last segment with 15 long, anteriorly directed, perianal setae. Pupa (after Haeselbarth, 1965*b*) with respiratory horn moderately long with 20–25 terminal spiracular openings; abdominal segments each with setose tubercles and definite pattern of small pigmented spots; caudal processes of last segment moderately long with strong spinules.

Biology: Larval habitats have been recorded for 7 Afrotropical species: stream margins, seepage pools with vegetation, margin of a water storage dam, from pupae collected among debris in backwaters of streams, from rice fields, and from plants of the water hyacinth, *Pistia stratiotes* L. De Meillon (1942: 13) reported of *Phaenobezzia pistiae* (Ingram & Macfie): 'This species is widely distributed over the Colony [Mozambique] and was certainly the commonest ceratopogonid present in Anopheline breeding places. Pupae were commonly found in lakes, backwaters of rivers and marshes and usually amongst vegetation.'

Distribution: Worldwide; 30 species.

Afrotropical species: The Afrotropical Catalogue lists 10 species; additions and corrections:

beni de Meillon & Wirth, 1983*a*: 379. South Africa.



Figs 389–401. Tribes Palpomyiini and Stenoxenini: 389–396, 401, *Stenoxenus coomani* Séguy; 397–398, *Palpomyia plebeia* (Loew); 399–400, *Palpomyia* sp.; 389, female antenna; 390, 397, female wing; 391, egg; 392, female palpus; 393, 398, female tarsi; 394, male parameres; 395, male genitalia, parameres omitted; 396, female head; 399, male genitalia; 400, female genitalia; 401, female abdomen, showing dorsal gland rods.

congolensis Vattier & Adam, 1966*b*: 758 (*Nilobezzia*). Rep. Congo. Synonym of *pajoti* (Vattier & Adam).
seychelleana Kieffer, 1911*b*: 350 (*Probezzia*). Seychelles.
troglophila Vattier & Adam, 1966*b*: 754 (*Nilobezzia*). Rep. Congo. Synonym of *pajoti* (Vattier & Adam).

Tribe Stenoxenini

Reference: Wirth & Ratanaworabhan, 1972*c*: 1368 (world revision).

Diagnosis: Body unusually slender and dorsoventrally flattened. Wing (Fig. 390) with one very narrow radial cell, usually extending to wing tip in ♀; r–m crossvein often very short, the cell between R and M very narrow or even obliterated. Eyes (Fig. 396) broadly separated. Legs long and slender, with fine setae; femora unarmed. ♀ claws very short, equal (Fig. 393). Eighth abdominal segment of ♀ (Fig. 401) narrowed distally with strong genital sclerotisation. Egg with peculiar frilled subapical collar (Mayer 1952: 583) (Fig. 391).

Genus *Stenoxenus* Coquillett

(Figs 389–396, 401)

Stenoxenus Coquillett, 1899: 61. Type species, *Stenoxenus johnsoni* Coquillett, by original designation.

Diagnosis: Moderately large midges, wing length 2,6–4,8 mm; body slender, dorsoventrally flattened. ♀ antenna much elongated, segments with stout setose setae, especially stout and numerous on segments 3–10 (Fig. 389); ♂ antenna with sparse plume. Palpus (Fig. 392) 4-segmented, the primitive fourth and fifth fused. Mesonotum broad and rounded anteriorly, without anterior tubercle. Legs long and slender, especially hind pair; femora unarmed; legs with vestiture of very fine erect setae; fourth tarsomeres cordiform; fifth tarsomeres of ♀ unarmed (Fig. 393). ♀ claws short and equal, each with small inner basal tooth (Fig. 393). Wing (Fig. 390) with crossvein r–m very short or obsolete, causing cell between veins R and M to appear narrow or disappear; costa long, extending to tip of wing in ♀; one radial cell; media sessile, in ♂ forking at level of r–m crossvein, in ♀ vein M2 characteristically elbowed. Squama thickened and darkened, often produced lobelike. ♀ abdomen (Fig. 401) with paired gland rods and eversible glands; one spermatheca. ♂ genitalia (Fig. 395) with ninth sternum short; ninth tergum short with well-developed apicolateral lobes; basistyle swollen mesally at base, slender distally; dististyle much elongated; aedeagus with high basal arch, tip slender; parameres (Fig. 394) fused distally in a single blade-like process with broadly rounded tip.

Immature stages: Egg (Fig. 391) with distinctive frilled collar at one end (Séguy, 1931*b*: 210). Larva and pupa undescribed.

Biology: *Stenoxenus pastorianus* was reared from soil taken from cracks in a sandstone plateau in Guinea which held shallow pools of water after rains.

Distribution: Pantropical; 18 species.

Afrotropical species:
pastorianus Clastrier, 1982*a*: 293. Rep. Guinea.

pauliani Vattier & Adam, 1966*b*: 767. Rep. Congo.
usutae de Meillon, 1959*a*: 355. South Africa; Liberia.

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INDEX TO GENERA AND SUBGENERA

(Synonyms in roman)

Species	*Page*
Acanthoconops Carter	55
Acanthohelea Kieffer	113
Afrohelea Wirth	86
Allohelea Kieffer	86
Alluaudomyia Kieffer	88
Ankistrodactylus Ingram & Macfie	121
Ankylohelea de Meillon & Wirth	90
Apelma Kieffer	78
Atrichopogon Kieffer	55
Bezzia Kieffer	133
Bothahelea Grogan & Wirth	91
Bothamia Meiswinkel	91
Brachypogon Kieffer	92
Calcarhelea Wirth & Grogan	93
Caloforcipomyia Saunders	60
Capehelea de Meillon & Wirth	93
Ceratohelea Wirth & Grogan	95
Clinohelea Kieffer	115
Congohelea Wirth & Grogan	96
Culicoides Latreille	83
Dasyhelea Kieffer	79
Dibezzia Kieffer	119
Dicrohelea Kieffer	123
Downeshelea Wirth & Grogan	96
Echinohelea Macfie	98
Euforcipomyia Malloch	61
Eukraiohelea Ingram & Macfie	113
Euprojoannisia Brethes	61
Fanthamia de Meillon	98
Forcipomyia Meigen	58
Hebetula Wirth & Debenham	120
Holoconops Kieffer	51
Homohelea Kieffer	121
Isohelea Kieffer	93
Jenkinshelea Macfie	121
Jenkinsia Kieffer	121
Johannsenomyia Malloch	123
Kolenohelea de Meillon & Wirth	100
Lasiohelea Kieffer	66
Lepidohelea Kieffer	68
Leptoconops Skuse	50
Luciamyia de Meillon	101
Mackerrasomyia Debenham	124
Macropeza Meigen	126
Macroptilum Becker	126
Mallochohelea Wirth	127
Metacanthohelea Wirth & Grogan	103
Metaforcipomyia Saunders	69
Microhelea Kieffer	70
Monohelea Kieffer	103
Neoculicoides Boorman & Lane	82
Neohelea Clastrier	105
Neosphaeromias Das Gupta & Wirth	127
Neostilobezzia Goetghebuer	113
Neurobezzia Wirth & Ratanaworabhan	116
Nilobezzia Kieffer	129
Notoceratopogon de Meillon & Downes	106
Palpomyia Meigen	134
Parabezzia Malloch	106
Paralluaudomyia Clastrier	108
Parapterobosca Harant *et al*	66
Pedilohelea De Meillon & Wirth	71
Pellucidomyia Macfie	116
Phaenobezzia Haeselbarth	135
Phytohelea Remm	71
Proforcipomyia Saunders	61
Proleptoconops Clastrier	53
Pterobosca Macfie	73
Rhinohelea de Meillon & Wirth	74
Saliohelea Wirth & Ratanaworabhan	74
Schizodactylus Ingram & Macfie	121
Schizoforcipomyia Chan & Le Roux	75
Serromyia Meigen	108
Sphaeromias Curtis	130
Stenoxenus Coquillett	137
Stilobezzia Kieffer	110
Stiloculicoides Wirth & Grogan	114
Styloconops Kieffer	55
Synthyridomyia Saunders	76
Tetrabezzia Kieffer	117
Thyridomyia Saunders	77
Trichohelea Goetghebuer	78
Warmkea Saunders	79
Xenohelea Kieffer	132